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The role of stress in determining community structure: Effects of hypoxia on an estuarine epifaunal community

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THE ROLE OF STRESS IN DETERMINING COMMUNITY STRUCTURE: EFFECTS OF HYPOXIA ON AN ESTUARINE EPIFAUNAL COMMUNITY

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

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by

Alessandra Sagasti

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

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ABSTRACT

Community models predict the effects of stress on community structure and processes. I tested the Menge and Sutherland 1987 model in an estuarine epifaunal community experiencing low oxygen stress, termed hypoxia. Epifauna, animals living on the surfaces of substrates, are ecologically important in many estuaries where hypoxia occurs, yet little is known about the effects of hypoxia on these communities.

Epifauna formed dense communities in the York River, a tributary of the Chesapeake Bay, USA, despite frequent hypoxia. Abundance and species composition was similar in two areas of the river, even though the downstream study area often experienced lower oxygen concentrations during hypoxic episodes than the upstream study area. Many dominant species exposed to high and low oxygen in the laboratory had a median lethal time (LT_{50}) in hypoxia greater than the duration of typical hypoxic episodes in the York River, suggesting that hypoxia may cause little mortality for many species in this system. Predation by a variety of taxa decreased during hypoxia in the laboratory, because many mobile predators had higher mortality than sessile prey, and because predation rates decreased. Peak recruitment of dominant taxa, and of total epifauna, in the York River occurred during neap tides in the downstream study area, coinciding with the lowest oxygen concentrations. In the laboratory, low oxygen decreased recruitment of dominant taxa, but some recruitment continued in hypoxia for most taxa, indicating that larvae of dominant epifauna are tolerant of hypoxia. Larval tolerance of hypoxia may allow communities to persist even though the recruitment season of many epifaunal species coincides with the peak season of hypoxia.

These findings supported some predictions of the consumer stress model, but not all. As predicted, when stress increased, the importance of disturbance for determining community structure increased, while the importance of predation decreased. Unlike predictions, stress changed recruitment rates in the laboratory. There were few effects of stress on abundance and diversity, possibly because in this system hypoxia is mild, brief, and because the species in this community can tolerate stress, colonize disturbed areas quickly, and grow quickly enough to complete life-cycles between hypoxic episodes.

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ROLE OF STRESS IN DETERMINING COMMUNITY STRUCTURE: EFFECTS OF HYPOXIA ON AN ESTUARINE EPIFAUNAL COMMUNITY

GENERAL INTRODUCTION

Community models

A fundamental goal of ecology is to understand the forces that structure communities. Community models synthesize the results of experiments and attempt to predict the effects of ecological forces such as environmental stress, species interactions, recruitment or environmental productivity on community structure (Zajac and Whitlatch 1985, Pearson and Rosenberg 1987, Menge and Olson 1990, Bertness and Callaway 1994). Models allow us to test our understanding of community processes in new systems and to predict the effects of anthropogenic and other stresses on biological resources.

Environmental stresses are mechanical forces (physical stress) or biochemical conditions (physiological stress) that decrease the fitness of organisms (Sousa 1984, Menge and Sutherland 1987). Disturbance occurs when stress leads to loss of biomass or death (Sousa 1984, Menge and Sutherland 1987). Many existing community models predict that environmental stress changes communities by increasing disturbance rates and changing the frequency of species interactions, but specific predictions of these models often contradict each other (Table 1).

In early models, authors proposed that moderate stress or disturbance could prevent competitive exclusion, thus increasing diversity (Grime 1977, Connell 1978, Huston 1979). These models also predicted that severe stress or disturbance can decrease diversity by limiting the community composition to tolerant species (Grime 1977, Connell 1978, Huston 1979). However, each of these models emphasized different mechanisms by which stress can affect community structure (Grime 1977, Connell 1978, Huston 1979). Specifically, Grime (1977) focused on evolutionary strategies, and suggested in his model that different strategies (competitive, stress-tolerant, or ruderal) determine whether organisms can survive

in stressful environments. In low stress environments, competitive species can exclude others, decreasing diversity. Increased stress leads to higher diversity as competitive exclusion slows, allowing stress-tolerant species and ruderal species, species that can invade disturbed habitats quickly, to survive. Diversity in high stress is limited to tolerant species.

The intermediate disturbance hypothesis (Connell 1978) focused on the observation that communities are often not at equilibrium. This hypothesis states that disturbance intermediate in frequency, spatial extent and intensity maintains species diversity. Following disturbances, new propagules colonize. As the interval between disturbance increases, more species can invade and diversity rises. As disturbance frequency declines further, competitive exclusion reduces diversity. Similarly, disturbances intermediate in spatial extent and intensity allow a high diversity of species to colonize and survive.

The dynamic equilibrium model built on earlier models, but also stressed the role of growth in determining the effect of stress on communities (Huston 1979, 1994). This model states that among functionally analogous species, high population growth rates lead to high rates of competitive exclusion. When growth is high in non-disturbed areas, competitive exclusion leads to low diversity. As growth rates decline, slower competitive exclusion rates lead to increased diversity. In highly disturbed environments, disturbance prevents competitive displacement, but since few species can survive diversity is also low.

In contrast to these models, the model of Pearson and Rosenberg (1978) suggested that organic enrichment, rather than stress, plays a central role in structuring benthic infaunal communities. In this model, stress is a secondary factor that modifies communities structured by food quantity and quality. Stress acts primarily by affecting the ability of individuals to survive and recruit. Under high stress, few organisms survive but space for recruitment is abundant. Organisms that can recruit under high stress (i.e. opportunists) dominate; diversity is low. As stress diminishes, a wider variety of species can survive and recruit, thus increasing diversity, while the abundance of opportunists decreases. Diversity is highest in intermediate stress because opportunists and other community members exist

together. At the lowest stress, communities are dominated by a suite of individuals less vulnerable to predation and accommodated to neighbors.

Menge and Sutherland's (1987) consumer stress model, a form of an environmental stress model (see further discussion in Menge and Olson 1990), extends the predictions of early models which focused on stress, by also considering the effects of stress on predation. In addition to effects on diversity, this model also predicts the effects of stress on the importance of several processes that organize communities. In this model, predators are assumed to be more susceptible to stress than sessile prey because mobile predators can leave stressed areas, and therefore are less likely to have evolved resistance to stress. In systems with high recruitment and high environmental stress, physical factors are most important in structuring communities because only tolerant species survive, and therefore diversity is low. As stress decreases, organisms become abundant and competition becomes important. Diversity is low if competitors exclude others (exclusion competition) and high if competitors can coexist (coexistence competition). Further environmental moderation leads to high predation, which can decrease the number of prey species and the importance of competition. Predators cause local extinctions and diversity drops. When recruitment is low, physical factors become relatively more important at all points on the stress gradient, because there is less interaction between species. Menge and Sutherland (1987) do not consider interactions between stress and recruitment.

In contrast to consumer stress models, prey stress models (Menge and Olson 1990) assume that prey are more susceptible to environmental stress than predators are because stress weakens prey defenses. For example, plants in a drought might produce fewer chemical defenses and thus become more susceptible to insect herbivory. Therefore, the importance of predation is proposed to increase as stress increases. Many experiments in the rocky intertidal support consumer stress models while many in terrestrial environments support prey stress models (Menge and Olson 1990). More research in a variety of

systems could determine why different communities demonstrate such diametrically opposed reactions to environmental stress.

Bertness and Callaway (1994) extend these previous models by proposing that in addition to affecting negative interactions between species, stress can affect positive interactions. They predict that positive interactions are important in systems with either harsh or very mild environmental conditions. When environments are stressful, positive interactions between species can alleviate the stress, for instance through habitat amelioration (Schaffner 1990, Hacker and Bertness 1999). In benign environments, predation is high and positive interactions between organisms can help them avoid predation (i.e. associational defenses (Hay 1986)).

Much of the evidence for widely accepted community models (i.e., Menge and Sutherland 1987) comes from forest or rocky intertidal habitats that experience stresses with small spatial extents, such as tree-falls, wave exposure, and battering by drift logs (Dayton 1971, Menge 1978, Sousa 1984). Large and regional scale stresses such as climate change may have unique effects (Menge and Olson 1990). For example, regional-scale variation affects larval and food supply (Underwood and Denley 1984, Roughgarden et al. 1988). Current models also rely primarily on evidence from physical stresses that have greater impacts on mobile predators than on sessile prey (Menge and Sutherland 1987). The impact of physiological stresses may be independent of trophic level (Menge and Olson 1990).

In this dissertation I investigate the ability of current community models to predict the effects of a physiological, regional-scale stress - hypoxia - on estuarine epifaunal communities. I focus on the consumer stress model (Menge and Sutherland 1987, Menge and Olson 1990) because it is widely accepted (Bertness and Callaway 1994), distinguishes between stress, disturbance and predation, and considers the effects of stress on diversity.

Hypoxia

Eutrophication and the subsequent depletion of water-column dissolved oxygen are two of the most important environmental stresses impacting coastal systems and their resident biological communities (Diaz and Rosenberg 1995). Hypoxia, the occurrence of low dissolved oxygen concentrations in the water column, is becoming more widespread and persistent globally due to accelerating anthropogenic eutrophication, which can increase oxygen depletion by increasing respiration (Officer et al. 1984, Paerl et al. 1998). Hypoxia can decrease growth, change behavior, and kill animals (Forbes and Lopez 1990, Diaz and Rosenberg 1995, Hagerman 1998). At the community level, hypoxia produces a shift from metazoan to microbial food webs (Jonas 1992, Malone 1992), with more energy transferred to microbes and less to commercially important fisheries species (Diaz and Rosenberg 1995). Communities exposed to hypoxia generally have increased abundances of opportunistic species and decreased abundances of large, bioturbating species (Holland et al. 1987, Schaffner et al. 1992, Ritter and Montagna 1999). Hypoxia also affects biological interactions such as predation (Breitburg et al. 1994). The effect of hypoxia on predation depends upon the duration, severity and frequency of hypoxia and the tolerance of predators. Areas with long-term, consistently low oxygen lack large mobile predators such as fish (Jorgensen 1980, Diaz and Rosenberg 1995). In areas with fluctuating oxygen levels, mobile predators temporarily leave hypoxic areas, then return when oxygen concentrations rise to take advantage of infaunal invertebrates that surfaced during the event (Pihl et al. 1992, Nestlerode and Diaz 1998). Some predators increase predation rates during hypoxia because they are more tolerant than their prey (Breitburg et al. 1994). Through its effects on disturbance and species interactions, hypoxia can change the diversity, biomass, species composition and function of benthic communities (Jorgensen 1980, Rosenberg et al. 1983, Llanso 1992, Schaffner et al. 1992, Ritter and Montagna 1999).

Epifaunal community structure

Although many studies have investigated infaunal communities exposed to hypoxia (e.g., Rosenberg et al. 1991, Llanso 1992, Arndt and Schiedek 1997, Gerhardt and Baden 1998), few have investigated the impacts of hypoxia on epifauna. Epifauna, animals that live on the surfaces of substrata, occur worldwide in marine (Harris 1990) and freshwater (Goldman and Horne 1983) habitats, and are abundant in estuaries (Abbe 1987, Schaffner et al. in press) where hypoxia is common (Diaz and Rosenberg 1995). Epifaunal animals such as barnacles, tunicates and hydroids are abundant in the Chesapeake Bay (Lippson and Lippson 1984, Schaffner 1990, Schaffner et al. in press). Currently, our knowledge of hypoxia's effects on benthic resources of the Chesapeake Bay does not include the epifaunal component (e.g., Holland et al. 1987, Dauer et al. 1992, Llanso 1992). Epifauna may be particularly susceptible to hypoxia because late-summer hypoxic episodes coincide with peak growth and recruitment periods in epifaunal communities (Abbe 1987), and because epifaunal species, which are not as exposed to low oxygen as infauna, may have evolved fewer mechanisms for tolerating hypoxic stress (Hagerman 1998). However, epifaunal species are abundant in some areas with low oxygen concentrations (Tunnicliffe 1981).

Classic experimental studies of community organization in ecology studied epifauna in rocky intertidal communities, and found that these communities are structured by recruitment, disturbance, competition and predation (Connell 1961, Paine 1966, Dayton 1971, Menge 1978). In temperate environments, epifaunal communities often experience rapid changes in species composition and abundance resulting from a combination of recruitment and mortality. Recruitment varies across seasons (Sutherland and Karlson 1977, Osman 1978, Underwood and Anderson 1994) and years (Sutherland and Karlson 1977, Abbe 1987) due to fluctuations in larval availability and settlement (Osman 1977, Turner and Todd 1993). The frequency and intensity of disturbance determine the amount of space available for recruitment, and can impact the diversity and species composition of

the epifaunal community (Sousa 1979, Kay and Keough 1981, Farrell 1989, Rheinhardt and Mann 1990). Competition is often intense in epifaunal communities because substrate space can be limiting (Connell 1961, Dayton 1971, Osman 1977). Good competitors can dominate space and create low diversity communities (Sousa 1979). Disturbance and predation on dominant competitors may free space and allow less competitive species to survive (Paine 1966, Lubchenco 1978, Petraitis et al. 1989).

Hypoxia might be an important structuring force in estuarine epifaunal communities because it affects each of these processes. Hypoxia can increase disturbance (Diaz and Rosenberg 1995), change recruitment (Widdows et al. 1989, Baker and Mann 1992, Breitburg 1992, but see Llanso 1991) and alter the outcome of species interactions (Sandberg 1994, Nestlerode and Diaz 1998). Hypoxia may therefore be a good example of regional-scale variation that can affect numerous community processes (Menge and Olson 1990).

Objectives

In this dissertation, I examine the effects of hypoxia on community structure and processes in epifaunal communities in the York River, Chesapeake Bay, USA. I use this system to investigate the effects of a regional scale stress on mortality, predation, recruitment and competition, and I relate results to predictions of consumer stress models. Specifically, applying the Menge and Sutherland (1987) consumer stress model to epifaunal communities experiencing hypoxia yields the following predictions:

> Prediction 1. Hypoxia will increase mortality and decrease the ability of sessile animals to capture and retain space, leading to lower abundances and lower species diversity in hypoxia than in high oxygen conditions. Species with low tolerance of hypoxia in the laboratory will experience the greatest reduction in abundance in hypoxic field conditions relative to higher oxygen conditions.

Prediction 2. Predators are highly susceptible to hypoxic stress and have decreased abundances in low oxygen conditions. As a result, predation is less important in low oxygen conditions than in high oxygen conditions.

Prediction 3. Recruitment rates are independent of hypoxia.

Prediction 4. Hypoxia will change the importance of competition. If hypoxia decreases predation on dominant space occupiers, it should increase the importance of competition. If hypoxia increases disturbance and decreases growth, it should decrease the importance of competition.

In the following chapters, I address each of these predictions.

In Chapter 1 I describe the epifaunal community in the York River and relate community structure to the occurrence and severity of hypoxia. I compare species composition in shallow areas, where hypoxia does not occur, to species composition in deep areas (15 m) where hypoxia is common. I also compare the percent cover of sessile species and abundance of mobile species in two deep areas, one of which experiences lower oxygen concentrations during hypoxic events.

In Chapter 2 I examine tolerance of hypoxia by epifaunal species, including effects on mortality, behavior, feeding rates and predation. I relate the tolerance of individual species to their abundance in hypoxic areas to investigate whether disturbance caused by hypoxia could influence the distribution of epifaunal species.

Chapter 3 discusses the effects of hypoxia on recruitment. I measured recruitment of sessile epifaunal species by deploying recruitment substrata in two areas with differing oxygen regimes, and allowing epifauna to recruit during periods of low oxygen (neap tides) and high oxygen (spring tides) in 1996 and 1997. I also conducted laboratory experiments

in which I exposed larvae of epifauna to high and low oxygen conditions. I combine the results of field and laboratory studies to examine the effects of a large scale stress on recruitment.

In Chapter 4 I discuss the importance of competition for structuring epifaunal communities in the York River, using correlations and a manipulative competitor removal experiment to search for evidence of competition for space by dominant sessile species.

Finally, a section on general conclusions evaluates the results of these studies relative to the predictions of consumer stress models, to ascertain whether consumer stress models correctly predicted the effects of hypoxia on epifaunal communities.

Table 1 - Predictions of community models regarding the effects of high stress/disturbance on community structure. The symbol ↓ indicates the importance of that process decreases as stress increases, ↑ indicates the importance of that process increases as stress increases. Arrows make no implications about the rates of increase or decrease; they simply give a qualitative description of overall model predictions.

	Competition	**Predation**	**Positive Interactions**	**Diversity**
Grime 1977	↓			high at intermediate stress
intermediate disturbance hypothesis; Connell 1978	↓			high at intermediate stress
Pearson and Rosenberg 1978		low at intermediate stress		high at intermediate stress
Huston 1979	↓			high at intermediate stress
consumer stress model; Menge and Sutherland 1987; Menge and Olson 1990	high at intermediate stress	↓		high at intermediate stress when coexistence competition; low at intermediate stress when exclusion competition
prey stress model; Menge and Olson 1990	↓	↑		
Bertness and Callaway 1994		↓	low at intermediate stress	

CHAPTER 1: EPIFAUNAL COMMUNITIES THRIVE IN AN ESTUARY WITH HYPOXIC EPISODES

Abstract

Epifaunal animals are a conspicuous and ecologically important component of some estuaries where low oxygen events (dissolved oxygen concentration in the water column ≤ 2 mg O_2 l^{-1}), termed hypoxia, are common. Although hypoxia is increasing in frequency and intensity in many estuaries, and is known to have adverse impacts on many infaunal organisms, little is known regarding its effects on epifauna. We characterized the abundance and species composition of sessile and mobile epifaunal assemblages in the York River, a tributary of the Chesapeake Bay, USA, during the summer hypoxia seasons in 1996 and 1997. We collected communities on artificial substrates in two areas of the river that have historically experienced different exposure to hypoxia. Despite frequent hypoxic stress, epifauna formed dense communities in both areas. Dominant species comprised a range of phyla and included the polychaetes *Polydora cornuta* and *Sabellaria vulgaris*, the bryozoans *Membranipora tenuis* and *Conopeum tenuissimum*, the tunicate *Molgula manhattensis*, the barnacle *Balanus improvisus*, the anemone *Diadumene leucolena* and the hydroids *Ectopelura dumortieri* and *Obelia bicuspidata*. Common mobile species included the nudibranchs *Cratena kaoruae* and *Doridella obscura*, the amphipods *Melita nitida* and *Paracaprella tenuis*, the polychaete *Nereis succinea* and the flatworm *Stylochus ellipticus*. We found few differences in species composition between the two areas, even though one area usually experienced lower oxygen concentrations during hypoxic events, suggesting that hypoxia does not exclude any epifaunal species in the York River. We did find

differences between the two study areas in percent cover and abundance of some species. While tunicates, hydroids and anemones were equally abundant in both areas during both study years, bryozoans and the polychaete *S. vulgaris* were more abundant in the area with generally higher oxygen, suggesting that they may be less tolerant of hypoxic stress. The polychaete *P. cornuta* was more abundant in the area that usually had lower oxygen. These results suggest that many epifaunal species have high hypoxia tolerance, and most epifaunal species found in the lower York River are able to survive in hypoxic areas. We conclude that, in contrast to earlier predictions, epifaunal species are not necessarily more susceptible to hypoxia than infaunal species in the York River. Epifaunal communities in areas with brief hypoxic episodes and moderate hypoxia (0.5 - 2 mg O_2 l^{-1}) can persist with little change in species composition, and with few changes in abundance, as oxygen concentrations fall.

Introduction

Epifaunal animals can be conspicuous and important components of estuarine faunas (Caine 1987; Schaffner 1990; Schaffner et al. in press). These animals serve as food for higher trophic levels (Kikuchi 1974; Pike and Lindquist 1994; Edgar and Shaw 1995), provide structural refuges from predation for fish and invertebrates (Levy and Sullivan 1994), and alter benthic-pelagic coupling processes by enhancing the deposition of organic matter (Haven and Morales-Alamo 1966) or benthic boundary-layer flow dynamics (Wright et al. 1987; Abelson et al. 1993). Additionally, some epifaunal suspension-feeders can reduce the effects of eutrophication and help to preserve water quality (Officer et al. 1982; Reeders et al. 1993).

Estuaries are increasingly exposed to low oxygen stress (hypoxia) (Diaz and Rosenberg 1995). Scientists differ on the exact definition of hypoxia, because oxygen requirements vary among animals (Modig and Olafsson 1998). Tyson and Pearson (1991) consider oxygen concentrations below 2 mg O_2 l^{-1} hypoxic, because at this level many fishes and other animals begin to feel stress. We will use this definition as a guideline, although there are few published data about oxygen concentrations that impact epifaunal animals. Hypoxia is spreading and growing more persistent globally because of anthropogenic eutrophication (Paerl et al. 1998), and currently occurs in most major estuaries in the United States (Diaz and Rosenberg 1995). Although many studies have shown major effects of hypoxia on infaunal animals (Diaz and Rosenberg 1995), little is known about the effects of hypoxia on epifauna. Among infaunal animals, hypoxia causes mortality (Rosenberg et al. 1991), changes in behavior (Diaz and Rosenberg 1995) and reductions in growth (Forbes and Lopez 1990). Hypoxia can also lead to decreased biomass and diversity (Dauer et al. 1992; Llanso 1992; Ritter and Montagna 1999), and can change the species abundance and species composition of infaunal assemblages (Gaston 1985; Holland et al. 1987b; Ritter and Montagna 1999).

Although many infaunal species are affected by hypoxic conditions, hypoxia tolerance varies among phyla and orders (Theede et al. 1969; Rosenberg et al. 1991) and even between species within a single order (McMahon and Russell-Hunter 1978). For example, many polychaetes, turbellarians, and bivalves are highly tolerant and can survive hypoxia for weeks (Theede et al. 1969; Rosenberg et al. 1991; Diaz and Rosenberg 1995) while many crustaceans and vertebrates are killed within hours or days (Diaz and Rosenberg 1995). The life history characteristics of infaunal species also affect their response to hypoxia. Opportunistic species with high reproductive rates and wide dispersal often exploit disturbed habitats (Grassle and Sanders 1973; Zajac and Whitlatch 1985). In estuaries, hypoxic disturbance can increase the abundance of small, short-lived species and decrease the abundance of large, long-lived species (Holland et al. 1987b; Llanso 1992; Schaffner et al. 1992). As a result, hypoxic areas often have lower diversity, abundance and biomass of large infauna, but higher density and biomass of small infauna (Dauer et al. 1992; Diaz and Rosenberg 1995).

The intensity (oxygen concentration) and duration of hypoxia also determine hypoxia's effects on infaunal animals (Forbes and Lopez 1990; Diaz and Rosenberg 1995). Many infaunal invertebrates can survive oxygen concentrations of 1 mg O_2 l^{-1} (Rosenberg et al. 1991), but few can survive a complete lack of oxygen (Diaz and Rosenberg 1995). Some species may tolerate mild hypoxia, but may not be able to survive when oxygen concentrations fall below a threshold oxygen level (Herreid 1980). Similarly, long hypoxic episodes have more severe consequences than short episodes (Modig and Olafsson 1998). While some species reduce metabolic rates and switch to anaerobic metabolism during short periods of hypoxia, and then recover as the oxygen increases (Hochachka and Somero 1984), extended periods of hypoxia kill even the most tolerant species by indirectly causing starvation (Diaz and Rosenberg 1995).

In contrast to infauna, little is known about the effects of hypoxia on epifauna, especially sessile epifaunal species or mobile species that are too small to escape from

hypoxic areas. Several unique characteristics of epifauna may make them more susceptible than infauna to hypoxia. First, epifaunal species live in the water column where they are less likely than sediment-dwelling infauna to encounter low-oxygen conditions, and where they may avoid the toxic effects of H_2S, which can increase the mortality of infauna during hypoxia (Hagerman 1998). Therefore, epifauna are less likely to have evolved adaptations to hypoxia and sulfide than infaunal species (Hagerman 1998). Second, epifaunal animals often live in dense, multispecies clumps which may increase mortality. For example, in low-flow environments the high density of animals in epifaunal clumps can lead to lower local oxygen concentrations. Although solitary mussels have high hypoxia tolerance, mussels living in clumps in a Danish fjord were among the first animals to die during a hypoxic episode because the high density of clumped mussels increased respiration and depleted oxygen locally (Jorgensen 1980). Stachowitsch (1984) also found that epifaunal species living in clumps had high mortality rates, but for different reasons. Sponges formed the primary structural component in these clumps. Once the sponges died, other species on the clumps died from prolonged contact with dead sponges. Finally, in many temperate estuaries like the Chesapeake Bay, peak growth and recruitment periods for epifauna occur in the summer (Abbe 1987), coinciding with hypoxic episodes. In contrast, peaks in growth and reproduction of infaunal animals in temperate estuaries often occur during spring and fall (Holland et al. 1987a; Diaz 1984) when oxygen is high. Therefore, epifaunal growth and recruitment may be more severely affected by hypoxia than those of infauna.

In this study, we explored the effects of hypoxia on epifaunal communities by characterizing the community of sessile and mobile epifauna during the summer when hypoxia is most common. Our objectives were 1) to compare the presence of species in deep areas, where hypoxia occurs, to the presence of species in shallow areas where hypoxia is absent, to determine if hypoxia may change the species composition of epifaunal communities in the York River, and 2) to compare the percent cover of sessile species and the abundance of mobile species in two deep areas of the York River with differing

exposure to hypoxia, to determine whether hypoxia may change the abundance of epifaunal species in this system. This study is among the first to characterize epifaunal communities exposed to hypoxia, and increases understanding of hypoxic effects on ecosystems.

Materials and Methods

Study location

We conducted our study in the York River, a tributary of the Chesapeake Bay, USA, where the timing and spatial extent of hypoxia are relatively predictable (Haas 1977; Kuo and Neilson 1987). A deep channel (about 15-20 m) runs from the mouth of the river to Gloucester Point (Fig. 1) (Kuo and Nielson 1987). During summer neap tides, low-oxygen water from the Chesapeake Bay often collects in this channel and can create hypoxic conditions below 9 m (Pihl et al. 1992). Upstream of Gloucester Point, shallower water depths and reduced contact with low-oxygen Bay water have historically resulted in the reduced occurrence of hypoxia (Sisson et al. 1991; Kuo et al. 1993). Tidal currents enhance mixing of bottom and surface waters in the York River. This tidal mixing can reoxygenate deep water and prevent hypoxia during spring tides but not during weaker neap tides. Therefore, hypoxia usually occurs during neap tides in the summer (Haas 1977; Kuo et al. 1993). At the surface, oxygen concentrations in the York River remain above 4 mg O_2 l^{-1} (Kuo et al. 1993).

Epifaunal assemblages are abundant in three habitats in the York River: relict oyster reefs, hydroid mounds and seagrass beds. Historically, the York River had extensive oyster reefs. Although healthy oysters are now rare, oyster shells still provide substrate for epifaunal attachment (Rheinhardt and Mann 1990). In addition, large accumulations (meters long) of the hydroid *Sertularia argentea* are widespread in muddy areas, and these features support diverse communities of epifauna (Schaffner et al. in press). York River

epifaunal species also attach to seagrass blades (Marsh 1973; Orth 1992) and can be found on the tube-tops of polychaetes and other infauna (Schaffner 1990).

Study design

To compare epifaunal communities growing in low-oxygen vs. high-oxygen conditions, we studied two areas within the York River (Fig. 1). Both areas have similar temperature and salinity (see Results), but the downstream area has historically experienced lower oxygen concentrations (Kuo et al. 1993). In each area, we established sampling stations located at randomly selected locations along the 15 m depth contour, where hypoxia occurs in the summer. In 1996 we placed 8 stations (described below) in each area for a total of 16 stations. In 1997 4 new stations were added for a total of 20 stations, with 10 stations in each area. In 1996, we lost the deployed equipment at half of the stations in each area as the summer progressed, due to collisions with boats or other problems. In 1997, each station was replaced as soon it was discovered lost and we ended the year with all stations intact.

Description of upstream and downstream areas

Besides differences in oxygen, other differences between the upstream and downstream areas may affect the interpretation of our results. The two areas differ in location, which may affect recruitment. The downstream area is closer to the Chesapeake Bay, which may be a source of epifaunal larvae for the York River. However, the species found in this study also live in shallows along the length of the York River; these adults may also provide a source of larvae that would be available throughout the entire river.

There are many similarities between the upstream and downstream areas. The two areas have comparable levels of chlorophyll (7-12 mg chlorophyll a l^{-1} upstream; 7-10 mg chlorophyll a l^{-1} downstream), nitrogen (1-5 μM NH_4^+ upstream; 1-6 μM NH_4^+ downstream) and phosphorus (0.5-1.5 μM PO_4^{3-} upstream; 0.5-1.5 μM PO_4^{3-}

downstream) in the summer (Sin 1998), suggesting that suspended food availability is similar. The sediment composition in each area may be important for species that build tubes using sediments. Sediment composition is similar in downstream and upstream areas, consisting of silty clay (Nichols et al. 1991). Both areas have similar current speeds (Lin, Jing. Virginia Institute of Marine Science (VIMS), Gloucester Pt., VA, USA, personal communication), with maximum current speeds of approximately 30-40 cm s^{-1} during spring tides (Sisson et al. 1991).

Collection of epifauna

Each sampling station consisted of a weighted PVC frame to which we attached test panels and a surface float (Fig. 2). In 1996 the PVC frame was placed approximately 0.5 m above the sediment. SCUBA divers observed that strong tidal currents could push these frames down into the mud, so in 1997 the PVC frames were placed 1-1.5 m above the sediment, where SCUBA divers confirmed that they remained suspended above the bottom.

Epifaunal communities were allowed to develop on 10 X 10 cm sanded PVC panels attached in a vertical orientation to the sediment surface. Each frame had 16 possible panel locations; we placed the test panels in randomly chosen locations on each frame. We placed one panel at each station in May 1996 and 1997, and then retrieved each station's panel monthly, and replaced it with a new, clean panel. Therefore, for each year and each station, a set of panels was retrieved in June, July, August and September, each of which was 1 month old. The retrieval of each set of panels was timed to follow a few days after neap tides, when hypoxic episodes are most likely to occur, however our timing was not always successful (Appendix 1).

To retrieve panels, we pulled the entire PVC frame and its attached panels out of the water by hand (1996) or with a mechanical winch (1997). Once on deck, panels were placed into 1-liter containers and held upright without dislodging or damaging epifauna. Individual containers were covered with 500-μm mesh to prevent mobile animals from

moving between panels and then kept in coolers with ambient sea water until we examined them in the laboratory.

In the laboratory, we estimated the percent cover of sessile epifaunal species using a point sampling technique (Sutherland and Karlson 1977). Briefly, 100 random points were traced onto a 10 X 10 cm transparent surface and suspended above a submerged panel. Live animals under each point were identified to the lowest possible taxon using a dissecting microscope. If more than one species fell under a point (if one species was growing on top of another), we counted all the species visible under that point. To estimate abundance of mobile epifauna, we scraped off the contents of each panel and sieved them through a 500-μm sieve, fixed the animals in 10 % buffered formalin with Rose Bengal stain, and identified and counted all mobile animals with a dissecting microscope.

To determine whether mobile animals such as crabs and nudibranchs became dislodged during retrieval, we also compared the number of mobile animals on panels retrieved by SCUBA to those on panels retrieved using a winch. Ten extra panels were placed at an upstream station in late June of 1997. Two months later, we retrieved half of these panels by SCUBA, placing each panel and its associated mobile fauna in a sealed bag before carrying it to the surface. We retrieved the remaining five panels from the surface using a winch. Panels were then processed as described above, but only mobile organisms were enumerated.

Oxygen measurements

To compare the physical environment of the upstream and downstream areas, we used a combination of data from ongoing VIMS studies and data from our stations to record the oxygen concentration, salinity and temperature in each area. In 1996, temperature, salinity and dissolved oxygen in the downstream area were measured hourly from a moored buoy east of Gloucester Point (Fig. 1). This buoy used an array of Hydrolab Datasonde Multiprobes to record conditions at multiple depths, including 13 m

and 16 m. To estimate conditions at the depth of our panels (14.5 m), we averaged the data from 13 m and 16 m.

In addition, we measured temperature, salinity and dissolved oxygen hourly at the upstream area in 1996 and in both areas in 1997 using a Hydrolab Datasonde Multiprobe at one station in each area (Fig. 1). The Hydrolab was suspended approximately 15 cm above the PVC frame with the sensors oriented toward the frame (Fig. 2). To prevent the sensors from becoming fouled, each Hydrolab was retrieved and replaced with a freshly calibrated Hydrolab weekly. After retrieving a Hydrolab, we tested it against standards to make sure it was still working properly. Salinity readings never differed from standards by more than 0.5 ppt, nor temperature by more than 0.71° C, nor oxygen concentration by more than 0.32 mg l^{-1}. However, we lost data periodically due to battery failure or sensor failures. In 1996, oxygen data was not available from the downstream area until June 21, and from the upstream area until June 15, so we are missing data during much of the first month of this study.

To estimate the variation in physical characteristics between stations within an area, we visited each station on at least 5 days each month throughout the summer of 1996. Water collected 1 m above the bottom with a Niskin bottle was measured for temperature and salinity using a thermometer and a refractometer (Leica model 10419). To measure oxygen concentration, an oxygen sensor (YSI Model 58, calibrated daily) was lowered to 1 m above the bottom. Because we could not visit stations simultaneously, these measurements span many hours and different stages of the tidal cycle.

Epifauna in shallow water areas

To document the species composition of epifauna in shallow, high-oxygen parts of the York River, we surveyed 10 X 10 cm PVC panels (n = 8) during the summer of 1995. These panels were attached to a PVC frame located approximately 1 m below the surface at the VIMS pier in Gloucester Point (Fig. 1). Two to three times per week from May

through September, we recorded the species composition of the sessile animals and scraped a 9-12 cm^2 area of a haphazardly chosen panel. We sieved the scraped community through a 500 μm sieve, fixed the sample in 10 % buffered formalin with Rose Bengal stain, and identified all animals to the lowest possible taxon with a dissecting microscope.

Statistical analysis

We tested for differences between upstream and downstream abundances of: 1) each sessile species that covered 5% of available panel space on at least one sampling date and 2) each mobile species that was present on at least 10% of panels on at least 2 sampling dates. For each species, a 2-factor Model 1 (fixed factor) ANOVA with factors date (panel retrieved in July, August or September) and location (upstream or downstream) was performed. Because hypoxia did not occur during the June 1997 deployment, and because we could not confirm whether it occurred during much of the June 1996 deployment, we did not include these months in the analyses. The response variable was either the percent cover (for sessile species) or the number of individuals per panel (for mobile species). Because many species were only abundant during part of the study, we included in the analysis only months when a species had at least 5% cover in at least one area of the river. A few species were only abundant during one month of the study; for these species we performed a t-test with location as the factor. To check the assumptions of these parametric tests, a Cochran's test for homogeneity of variance (Underwood 1997) and a Shapiro-Wilkes test for normality (Zar 1996) were performed for each species. If a species did not meet the assumptions of normality and homogeneity of variance, we transformed the data by log (x+1) or by square root (x + 0.5) and tested again for normality and homogeneity of variance (Zar 1996). All species met both assumptions of normality and homogeneity of variance before we performed ANOVAs or t-tests.

In this study, we test the same null hypothesis (that there is no difference between upstream and downstream areas) for various species. Each statistical test that we have

performed is valid for each species separately, and we consider an individual test significant if $\alpha \leq 0.05$. However, the overall experiment error may have an increased likelihood of Type I errors, and to compensate for this problem we have adjusted alpha values using sequential Bonferroni corrections (Peres-Neto 1999). Thus, for each species we report the significance from uncorrected ANOVAs or t-tests, and the significance after sequential Bonferroni corrections (Peres-Neto 1999). We hope that reporting the results arrived at by the two methods will better illustrate which species have the strongest evidence of differences between upstream and downstream, and which species have weaker evidence.

To test for differences between panels retrieved by SCUBA and panels retrieved from the surface using a winch, we performed t-tests on the abundance of each species, with the method of retrieval as the factor. We used Cochran's homogeneity of variance test (Underwood 1997) and a Shapiro-Wilkes normality test (Zar 1996) to check the assumptions of parametric analysis. When a species did not meet assumptions, we transformed the data by log(x+1) or by square root (x + 0.5) until the data met assumptions. Three species were found on panels retrieved by winch, but not on panels retrieved by SCUBA. For these species we could not meet the assumptions of t-tests, and instead we compared the 95% confidence intervals of samples collected by winch to see if they were significantly different from zero.

Results

Physical environment of upstream and downstream areas

In 1996, hypoxic episodes (DO $\leq$ 2 mg O_2 l^{-1}) were most severe during neap tides in late June and July (corresponding with July and August deployments), and less severe oxygen depletion occurred during neap tide in late August (Fig. 3). Hypoxia also occurred in September for brief periods, but was not severe enough to cause average daily oxygen concentrations to fall below 2 mg O_2 l^{-1} (Fig. 3). During the June and July episodes,

average daily oxygen concentrations remained below 2 mg O_2 l^{-1} for approximately 1 week (Fig. 3). Hypoxia occurred in both upstream and downstream areas, but reached lower concentrations downstream. For example, we can compare the number of days with minimum oxygen concentrations < 2 mg O_2 l^{-1}, < 1 mg O_2 l^{-1} and < 0.5 mg O_2 l^{-1} upstream and downstream during days when oxygen data is available for both areas. We find lower oxygen downstream during the July (< 2 mg O_2 l^{-1}: 11 days upstream, 10 days downstream; < 1 mg O_2 l^{-1}: 0 days upstream, 6 days downstream; < 0.5 mg O_2 l^{-1}: 0 days upstream, 4 days downstream), August (< 2 mg O_2 l^{-1}: 9 days upstream, 13 days downstream; < 1 mg O_2 l^{-1}: 0 days upstream, 6 days downstream; < 0.5 mg O_2 l^{-1}: 0 days upstream, 3 days downstream) and September (< 2 mg O_2 l^{-1}: 7 days upstream, 10 days downstream; < 1 mg O_2 l^{-1}: 1 day upstream, 4 days downstream) deployments. There was not enough data to compare oxygen concentrations during the June deployment.

Hypoxia was less common in 1997 (Fig. 3), with only one major hypoxic episode in mid-July, and a less severe episode in mid-August, corresponding with July and August deployments. Again, hypoxia occurred in both areas of the river, but was more severe downstream. Once more, we can compare the number of days with minimum oxygen concentrations of < 2 mg O_2 l^{-1}, < 1 mg O_2 l^{-1} and < 0.5 mg O_2 l^{-1} upstream and downstream during days when oxygen data is available for both areas. We find lower oxygen downstream during the July (< 2 mg O_2 l^{-1}: 3 days upstream, 5 days downstream; < 1 mg O_2 l^{-1}: 1 day upstream, 2 days downstream; < 0.5 mg O_2 l^{-1}: 0 days upstream, 1 day downstream), August (< 2 mg O_2 l^{-1}: 5 days upstream, 14 days downstream; < 1 mg O_2 l^{-1}: 3 days upstream, 5 days downstream; < 0.5 mg O_2 l^{-1}: 0 days upstream, 2 days downstream) and September (< 2 mg O_2 l^{-1}: 2 days upstream, 8 days downstream) deployments. There was no hypoxia during the June deployment.

Temperature and salinity were similar from year to year (Fig. 5). Temperatures rose steadily from 15 °C in May to approximately 26 °C in September (Fig. 5). Salinity

averaged 20 ppt, falling to 16 ppt during spring tides and rising to 24 ppt during neap tides (Fig 5).

Because of travel time between stations, measurements at stations within a single area of the river were separated by hours and were taken at different stages of the tidal cycle. Still, measurements of temperature, salinity and oxygen were similar, suggesting that physical conditions are alike at different stations within an area. Temperature varied by less than 1° C during 70% of our measurements, and never differed by more than 3° C. Salinity varied by less than 2 ppt during 88% of our measurements, and never differed by more than 4 ppt. Oxygen concentrations varied more, because oxygen at a single location often changed by up to 4 mg O_2 l^{-1} within just a few hours, less time than it took for us to measure oxygen concentrations at all stations. However, within a single area (upstream or downstream), oxygen at stations that we measured within 30 minutes of each other varied by 0.4 mg O_2 l^{-1} or less during 75% of our measurements.

Epifaunal communities

During this study, the species composition of epifauna at our stations (15 m deep) was similar to that of shallow parts of the York River (Table 1). While shallow and deep areas shared 44 species, only 8 species were found exclusively in shallow areas and 2 species were found exclusively in deep areas (Table 1). Although there were many rare species, the community was often dominated by a few species. For example, of 17 sessile taxa present on deep panels (Table 1), only 8 species in 1996 and 9 species in 1997 covered 5% of available panel space on at least one sampling date during the study (Fig. 7). The average number of species per panel was similar in both areas in the river (upstream and downstream) (Fig. 6).

There were no significant differences in the number of mobile epifaunal animals between panels pulled through the water column with a winch and panels retrieved by SCUBA ($p > 0.5$, t-tests) (Table 2), suggesting that mobile epifauna such as snails,

nudibranchs and crabs cling to panels rather than becoming dislodged during retrieval. Three taxa were only found in winch treatments, and could not be compared using t-tests (Table 2). However, for these taxa the 95% confidence intervals (mud crabs -0.17 to 2.57; *Mitrella lunata* -0.19 to 0.59; pycnogonids -0.38 to 1.18) include zero, suggesting that they also did not differ between winch and SCUBA treatments. Thus, our data on mobile species from panels retrieved by winch are unlikely to be biased.

Abundance of many epifaunal species differed significantly among dates in this seasonal environment (Table 3), with similar trends in 1996 and 1997 (Fig. 7 and 8). Early in the summer of both years, the polychaete *Polydora cornuta* constructed tubes that formed thick carpets on top of the barnacle *Balanus improvisus* and the tunicate *Molgula manhattensis*. Over the course of the summer, bryozoans (*Membranipora tenuis* and *Conopeum tenuissimum*), the polychaete *Sabellaria vulgaris*, the anemone *Diadumene leucolena* and hydroids (*Obelia bicuspidata* and *Ectopleura dumortieri*) increased in abundance, while *P. cornuta* became less abundant. Most species were able to grow on top of other species, and the community became a thick, complex matrix of several layers. Among mobile epifauna (Fig. 8), the oyster flatworm *Stylochus ellipticus* was abundant early in the summer of 1997. The clamworm *Nereis succinea* was common throughout both summers. The nudibranch *Doridella obscura* was particularly abundant when its prey, encrusting bryozoans, were common in mid-summer. We found a number of species that seemed to be associated with *Obelia bicuspidata* and *Ectopleura dumortieri*, including the nudibranchs *Cratena kaoruae* and *Tenellia* sp., the caprellid amphipod *Paracaprella tenuis*, and several other amphipods.

Of the dominant sessile species (8 total in 1996 and 7 total in 1997) present during deployments when hypoxia occurred, percent cover of 5 species in 1996 and 3 species in 1997 differed significantly between upstream and downstream sites (Table 3, Fig. 7). The bryozoan *Membranipora tenuis* and the polychaete *Sabellaria vulgaris* were more abundant in the upstream area, with generally higher oxygen, during both years (Table 3).

The barnacle *Balanus improvisus* and the bryozoan *Conopeum tenuissimum* were also significantly more abundant upstream during 1996 (Table 3), but were not tested in 1997 because they weren't abundant during months with hypoxia. Interestingly, however, the sessile species with the greatest percent cover in this community either reached greater abundance downstream or had similar abundance in the two areas (Table 3, Fig. 7). *Diadumene leucolena*, *Molgula manhattensis* and *Obelia bicuspidata* had similar abundance upstream and downstream during both years (Table 3). Together, these species comprised more than 80% cover in July, August and September (Fig. 7) of both years. In addition, *Ectopleura dumortieri* showed no significant differences in 1997 (Table 3). During both years, *Polydora cornuta* was more abundant in the downstream area, with significant interaction effects suggesting that downstream/upstream differences were greatest during July when it was most abundant (Table 3).

Of the dominant mobile species (5 total in 1996 and 6 total in 1997), abundance of only 1 species in 1996 and 2 species in 1997 differed significantly between upstream and downstream sites (Table 3, Fig. 8). The nudibranch *Doridella obscura* was more abundant upstream, where oxygen was generally higher, during both years (Table 3, Fig. 8). In 1997, the caprellid amphipod Paracaprella tenuis was more abundant downstream, where oxygen was generally lower (Table 3, Fig. 8).

When we adjust significance with sequential Bonnferoni corrections (Peres-Neto 1999), we find that, for some species, the differences between upstream and downstream become insignificant (Table 3). For example, in 1996 differences between upstream and downstream for 1 species, the bryozoan *Membranipora tenuis* , became insignificant, but differences remained significant for 5 other species (Table 3). In 1997, differences between upstream and downstream became insignificant after sequential Bonferroni corrections for all species except the polychaete *Polydora cornuta* (Table 3).

Discussion

In the lower York River, epifaunal animals appear to be highly tolerant of hypoxia. Hypoxic episodes with dissolved oxygen concentrations ranging from 0.2 mg O_2 l^{-1} to 2 mg O_2 l^{-1} occurred approximately once a month throughout both summers, and lasted for 5-7 days at a time. In spite of these episodes, epifaunal animals formed dense, spatially complex communities of sessile and mobile species that included a range of phyla. The number of species present at 15 m, where hypoxic episodes occurred, was similar to the number of species in shallow, high-oxygen parts in the York River, suggesting that periodic hypoxia characteristic of the York River does not exclude most epifaunal species.

The ability of epifaunal animals in the York River to persist in hypoxic areas appears to be comparable to that of infaunal animals. Although hypoxia produces dramatic changes in the abundance, diversity and species composition of infaunal communities in many systems around the world (Diaz and Rosenberg 1995; Ritter and Montagna 1999), it has limited effects on infaunal community structure in the York River, probably because hypoxic episodes are brief (Diaz et al. 1992). Hypoxic episodes in the lower York River that last less than 1 week and are mild (oxygen concentrations remain above 0.5 mg O_2 l^{-1} except for during a few hours per day) cause changes in the behavior, growth and production of infaunal animals, but, as we also found for the epifaunal community, these episodes do not alter species composition or diversity (Diaz et al. 1992). Longer episodes of hypoxia or more severe oxygen depletion, caused by unusual events such as Tropical Storm Agnes in 1972, can change community structure of infauna in the York River (Boesch et al. 1976), and may also have larger impacts on epifauna.

Although we found the severity of hypoxia to be somewhat higher downstream than upstream during hypoxic episodes, these differences apparently did not alter the species composition of epifaunal assemblages dramatically. We did find differences in percent cover or abundance of some species between the upstream and downstream areas,

suggesting that hypoxia may have subtler effects on the epifaunal community. Many of the species that differed between the two areas were more abundant upstream (4 our of 5 in 1996, 2 out of 3 in 1997), but others were more abundant downstream. This suggests that hypoxia has species-specific effects on epifauna, supporting physiological studies that show substantial differences in hypoxia tolerance between related taxa (Diaz and Rosenberg 1995).

During both study years, several species had similar percent cover upstream and downstream. There are several possible reasons why these species were equally abundant in both areas. First, the difference in oxygen concentration between upstream and downstream areas may have been too small to change the abundance of these species. Hypoxia occurred in both areas but was approximately 0.5 mg O_2 l^{-1} lower in the downstream area during hypoxic episodes. At oxygen concentrations below 1 mg O_2 l^{-1}, small oxygen differences (0.1 mg O_2 l^{-1} or greater) produce large changes in the behavior and survival of many infaunal animals (Diaz and Rosenberg 1995). Similarly, small oxygen differences (<0.15 mg O_2 l^{-1}) can significantly change mortality and behavior of epifaunal fish (Breitburg 1992). Thus, other studies suggest that the oxygen differences we observed between sites could have been important for epifaunal animals. If so, the differences were not sufficient to cause changes in percent cover. Second, some species may be especially tolerant of hypoxia. At least one species, the anemone *Diadumene leucolena*, can switch to anaerobic metabolic pathways during hypoxia (Beattie 1971), which may allow it to tolerate low oxygen concentrations for long periods of time. Another explanation for the similarity in abundance upstream and downstream for some species involves growth rates relative to our sampling frequency. Hypoxia may change abundance, but because hypoxic events are brief, populations might recover between episodes. Recovery could occur through growth and migration of existing animals or by recruitment. Previous studies in the Chesapeake Bay show that many epifaunal species grow quickly, reaching adult size and maturity in just weeks (Abbe 1987). We have also observed rapid growth of many species; for example the

tunicate *Molgula manhattensis* larvae can settle and grow to a diameter of 1-2 cm in just one week. Therefore, some epifaunal species may grow quickly enough between hypoxic episodes to compensate for any effect of hypoxia on mortality or the ability to capture space. If species were killed by hypoxia they could have recovered through recruitment, with larvae from shallow parts of the river colonizing deep areas following hypoxia.

During both years, the tube-building worm, *Polydora cornuta*, was more abundant in the downstream area with generally lower oxygen. At times, *P. cornuta* covered almost 100% of downstream space, with tubes forming a carpet several centimeters thick (Fig. 9). In 1996, *P. cornuta* was most abundant in June and July deployments. Although we don't know the oxygen history of June panels, high abundance in July followed the worst recorded hypoxic episode. In 1997, *P. cornuta* was most abundant in July, again following the worst hypoxic episode. The success of *P. cornuta* in the downstream area may be explained by its life history characteristics. *P. cornuta* also lives in degraded and disturbed areas in other systems (Noji and Noji 1991; Zajac 1991), and is dominant throughout the Chesapeake Bay in early summer (Otsuka and Dauer 1982). Often, it is the first species to colonize after disturbances (Noji and Noji 1991) suggesting that it is opportunistic and takes advantage of disturbances to capture space. We observed highly rapid growth and recruitment of *P. cornuta*; lawns of *P. cornuta* tubes 2-3 cm thick can develop in just a few weeks of exposure (Fig. 9). The short life span and high fecundity of *P. cornuta* (Noji and Noji 1991) may make it especially adapted for living in a stressful area like the lower York River. Similarly, infaunal species with fast growth and high recruitment often dominate in hypoxic areas (Diaz and Rosenberg 1995).

Each year, some sessile species were more abundant upstream. Some of these species may require higher oxygen concentrations. They may also have slower growth or recruitment that could prevent them from recovering from hypoxia as quickly as other species.

Mobile species also showed a variety of responses, with *Doridella obscura* more abundant upstream during both years, *Paracaprella tenuis* more abundant downstream in 1997, and the majority of species showing no difference between sites. In addition to possible mechanisms used by sessile species to survive hypoxia, mobile animals may survive hypoxic episodes by migrating to shallow areas during hypoxia and returning after oxygen concentrations rise. In this study, they may simply have crawled up the ropes connecting each station to the surface, avoiding periods of low oxygen (but we did not gather evidence to support or refute this possibility).

It is also possible that differences between upstream and downstream areas were related to some factor other than oxygen. The two areas experience similar temperatures, chlorophyll concentrations, nutrient concentrations, sediment composition and current speeds. Epifaunal adults live in shallow areas along the length of the river, suggesting that larvae are available throughout the river (but their relative abundance may differ). Although salinity differed slightly (0-3 ppt) between the two sites in August and September 1996 (Fig. 5), these differences were probably too small to change species abundance between our sites, because salinities at both sites were well within the tolerance range of most epifaunal species in the York River. For example, many York River epifaunal species live in salinities ranging from oligohaline to polyhaline, including the barnacle *Balanus improvisus*, the polychaetes *Polydora cornuta* and *Nereis succinea*, the flatworm *Stylochus ellipticus* and the anemone *Diadumene leucolena* (Cory 1967). Both bryozoans (*Membranipora tenuis* and *Conopeum tenuissimum*) common in this study have a lower salinity limit of 6 ppt and an upper limit near euhaline conditions (Osburn 1944), while the tunicate Molgula manhattensis has a salinity range from 5 ppt to polyhaline (Cory 1967). The polychaete *Sabellaria vulgaris* has a distribution from mesohaline to polyhaline regions (Cory 1967), and the nudibranchs *Doridella obscura* and *Cratena kaoruae* both live in salinities as low as 9 ppt (Vogel 1977). Among the common sessile species in this study, only the hydroids *Obelia bicuspidata* and *Ectopleura dumortieri* are restricted to

narrow salinity ranges (Calder 1971), but we found no significant effects of location on abundances of these species (Table 3). Among the common mobile epifauna in this study, only the amphipods *Melita nitida* and *Paracaprella tenuis* are near the limit of their salinity range at our sites (Feeley and Waas 1971) (Table 3). Thus, for most species it is unlikely that salinity differences between sites changed species abundance. Hypoxia is a more likely cause of the differences between upstream and downstream for a couple of reasons. First, hypoxia is the most obvious physical difference between the two areas, and has been shown to be an important factor in other communities around the world (Diaz and Rosenberg 1995). Second, for many of the epifaunal species of the York River, we have observed significant mortality after exposure to hypoxia (1 mg O_2 l^{-1}) for several days (personal observation), suggesting that hypoxia can have important effects on these species.

This study was among the first to examine the effect of hypoxia on epifaunal communities, and we found similarities with results from infaunal communities. Although previous authors have suggested that epifaunal species may be particularly susceptible to hypoxic stress (Jorgensen 1980; Stachowitsch 1984; Hagerman 1998), we found that, like many infaunal species, many dominant epifaunal species appear to have high tolerance for hypoxia.

Epifauna are important ecological components of estuaries. As hypoxia becomes increasingly widespread and persistent (Diaz and Rosenberg 1995), the species composition of estuaries may change. This study suggests that, unlike earlier predictions, epifauna are not necessarily more susceptible to oxygen stress than infauna. Epifaunal communities may persist with relatively unchanged species composition, but with some changes in abundance, as oxygen concentrations fall, at least in areas where hypoxia is relatively mild and occurs for only short episodes.

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Table 1. Presence / absence of epifauna at shallow (S) (< 2 m) and deep (D) (15 m) sites in the York River from May through September. An X indicates that the species is present at that depth.

Species	S	D	Species	S	D	Species	S	D
Annelids			Flatworms			Cnidarians		
Eteone heteropoda	X	X	*Euplana gracilis*	X	X	*Clytia cylindrica*	X	X
Hydroides dianthus	X	X	*Stylochus ellipticus*	X	X	*Diadumene leucolena*	X	X
Nereis succinea	X	X				*Ectopelura dumortieri*	X	X
Podarkeopsis levifuscana		X	Crustaceans			*Haliplanella luciae*	X	X
Polydora cornuta	X	X	*Balanus eburneus*	X		*Obelia bicuspidata*	X	X
Sabella microphthalma	X	X	*Balanus improvisus*	X	X	*Schizotricha tenella*	X	
Sabellaria vulgaris	X	X	*Callinectes sapidus*	X	X	*Sertularia argentea*	X	X
Lepidonotus sublevis	X[1]	X	*Caprella penantis*	X				
			Corophium sp.	X	X	Molluscs		
Bryozoans			*Edotea triloba*	X	X	*Cratena kaoruae*	X	X
Anguinella palmata	X	X	*Erichthoneus brasiliensis*	X	X	*Doridella obscura*	X	X
Bowerbankia gracilis	X	X	*Eurypanopeus depressus*	X	X	*Mitrella lunata*	X	X
Conopeum tenuissimum	X	X	*Gammarus mucronatus*	X	X	*Tenellia* sp.	X	X

Membranipora tenuis	X	X	*Melita appendiculata*	X	X	*Urosalpinx cinerea*	X	X
			Melita nitida	X	X	*Eupleura caudata*	X	
Sponges			*Neopanope sayi*	X	X			
Halichondria bowerbanki	X		*Paracaprella tenuis*	X	X	Pycnogonids		
Haliclona spp.	X		*Parametopella cypris*		X	unidentified pycnogonid	X	X
Lissodendoryx carolinesis	X		*Pleusymptes glaber*	X	X			
Microciona prolifera	X	X	*Rhithropanopeus harrisii*	X	X	Foraminifera		
			Stenothoe minuta	X	X	*Milliamina fusca*	X	X
Nemertea								
unidentified nemertean	X	X	Tunicates					
			Botryllus schlosseri	X				
			Molgula manhattensis	X	X			

[1]We observed this worm in shallow water, but do not have a preserved specimen to confirm identification.

Table 2. The mean number of mobile epifauna per panel (± 1 standard deviation) on panels pulled up through the water column with a winch (n=5) and collected by hand using SCUBA (n=5). All panels were located at an upstream station and had been deployed in the river from 6/25/97 to 8/25/97. The t-statistic and p-value for t-tests comparing panels retrieved by winch and panels retrieved by SCUBA are reported. Three species were found in only one treatment and did not meet the assumptions of t-tests; no statistical tests were performed for these species.

Species	Winch	SCUBA	T-statistic	P
Cratena kaoruae	3.2 (2.4)	1 (1.7)	-1.67	0.14
Erichthoneus brasilensis	0.4 (0.5)	0.6 (0.9)	0.43	0.68
mud crab	1.2 (0.7)	0 (0)		
Melita nitida	8.8 (7.1)	5.6 (1.5)	-0.51	0.63
Mitrella lunata	0.2 (0.2)	0 (0)		
Nereis succinea	88.8 (15.0)	83.6 (20.6)	-0.46	0.66
Paracaprella tenuis	1280 (998.0)	170 (130.2)	-2.47	0.69
Parametopella cypris	0.6 (0.9)	0.2 (0.4)	-0.89	0.41
pycnogonid	0.4 (0.4)	0 (0)		
Pleusymptes glaber	8.2 (7.8)	1.8 (2.2)	-1.71	0.13
Stenothoe minuta	2.4 (1.5)	2.4 (2.6)	0	1.0
Stylochus ellipticus	0.6 (0.9)	0.2 (0.5)	-0.89	0.49

Table 3. The results of ANOVA tests for differences in percent cover of sessile species or abundance per panel of mobile species between upstream and downstream areas (location) and among dates during 1996 and 1997. Date was not included as a factor for species that were abundant (greater than 5% cover in at least one area) on only a single date in a given year. Non-significant p-values ($\alpha > 0.05$) are marked NS. P-values marked with an asterisk are significant even after sequential Bonferroni correction.

Species	Dates Analyzed	Date		Location		D * L	
		F	P	F	P	F	P
1996 Sessile							
Balanus improvisus	July			19.70	0.002*		
Conopeum tenuissimum	July			12.49	0.008*		
Diadumene leucolena	August-Sept	0.83	0.038	4.40	NS	0.55	NS
Membranipora tenuis	August			8.01	0.025		
Molgula manhattensis	June-July, Sept	21.13	<0.001*	0.52	NS	0.20	NS
Obelia bicuspidata	July-August	2.14	NS	2.43	NS	0.17	NS
Polydora cornuta	June-August	177.39	<0.001*	13.01	0.003*	9.69	0.007*
Sabellaria vulgaris	July-August	1.47	NS	13.68	0.002*	0.03	NS

1996 Mobile							
Cratena kaoruae	July-Sept	1.19	NS	2.49	NS	0.84	NS
Doridella obscura	June-August	0.54	NS	32.15	<0.001*	2.34	NS
Melita nitida	July-Sept	1.76	NS	0.15	NS	0.12	NS
Nereis succinea	June-Sept	16.79	<0.001*	3.83	NS	2.73	NS
Paracaprella tenuis	July-Sept	9.54	0.001*	0.50	NS	3.47	NS
1997 Sessile Species							
Diadumene leucolena	August-Sept	23.05	<0.001*	<0.001	NS	3.77	NS
Ectopleura dumortieri	August-Sept	0.01	NS	1.19	NS	0.12	NS
Membranipora tenuis	July-Sept	4.61	0.016*	4.15	0.048	<0.001	NS
Molgula manhattensis	July-Sept	17.05	<0.001*	0.090	NS	3.23	NS
Obelia bicuspidata	July-Sept	17.05	<0.001*	0.09	NS	3.23	NS
Polydora cornuta	July, Sept	67.86	<0.001*	26.85	<0.001*	23.23	<0.001*
Sabellaria vulgaris	August			6.07	0.027		
1997 Mobile Species							
Cratena kaoruae	August-Sept	2.93	NS	0.13	NS	0.02	NS

Doridella obscura	July-Sept	22.54	<0.001*	5.51	0.024	0.71	NS
Nereis succinea	July-August	9.50	<0.001*	1.61	NS	2.64	NS
Paracaprella tenuis	July-Sept	71.24	<0.001*	6.27	0.016	0.24	NS
Stylochus ellipticus	July-August	10.97	0.003*	0.35	NS	3.46	NS
Tenellia sp.	July-Sept	0.12	NS	0.57	NS	2.34	NS

Fig. 1. Sampling stations in the York River, Virginia. In each area, we placed stations at randomly chosen locations along the 15 m depth contour.

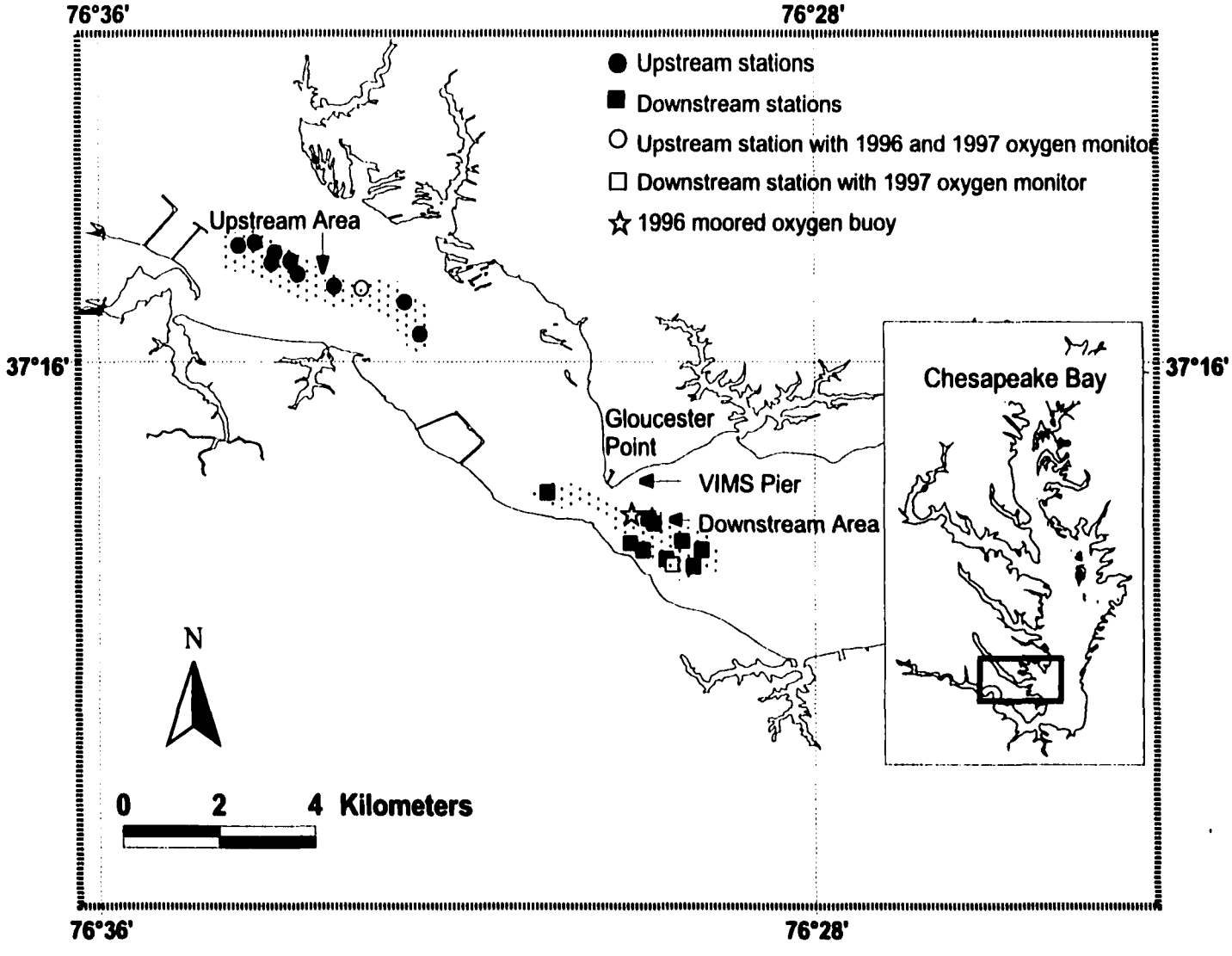


Fig. 2. Schematic of equipment at a station, showing the location of PVC frames, panels and floats. We also show the location of a Hydrolab oxygen meter which was placed on selected stations (see Fig. 1).

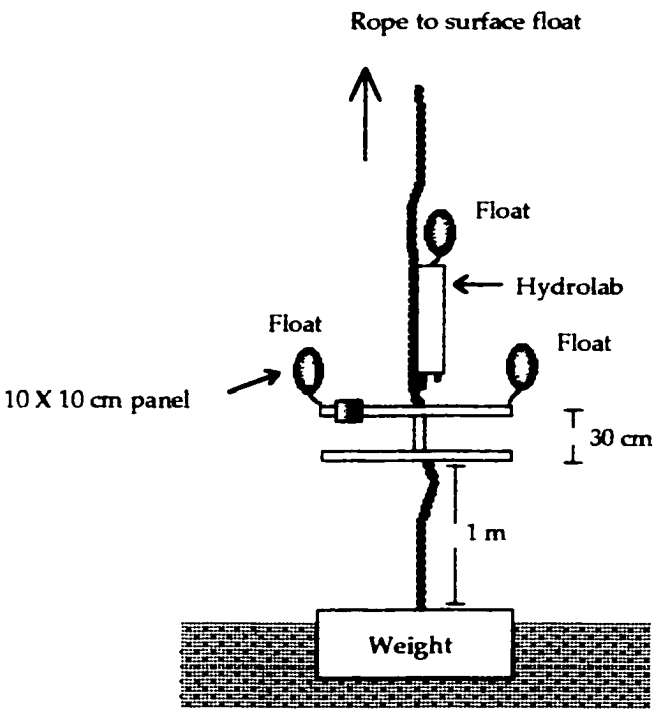


Fig. 3. Daily dissolved oxygen concentration for upstream and downstream areas in 1996 and 1997. We averaged hourly dissolved oxygen measurements to provide daily averages. All oxygen concentrations below the dashed reference line (2 mg O_2 l^{-1}) are considered hypoxic.

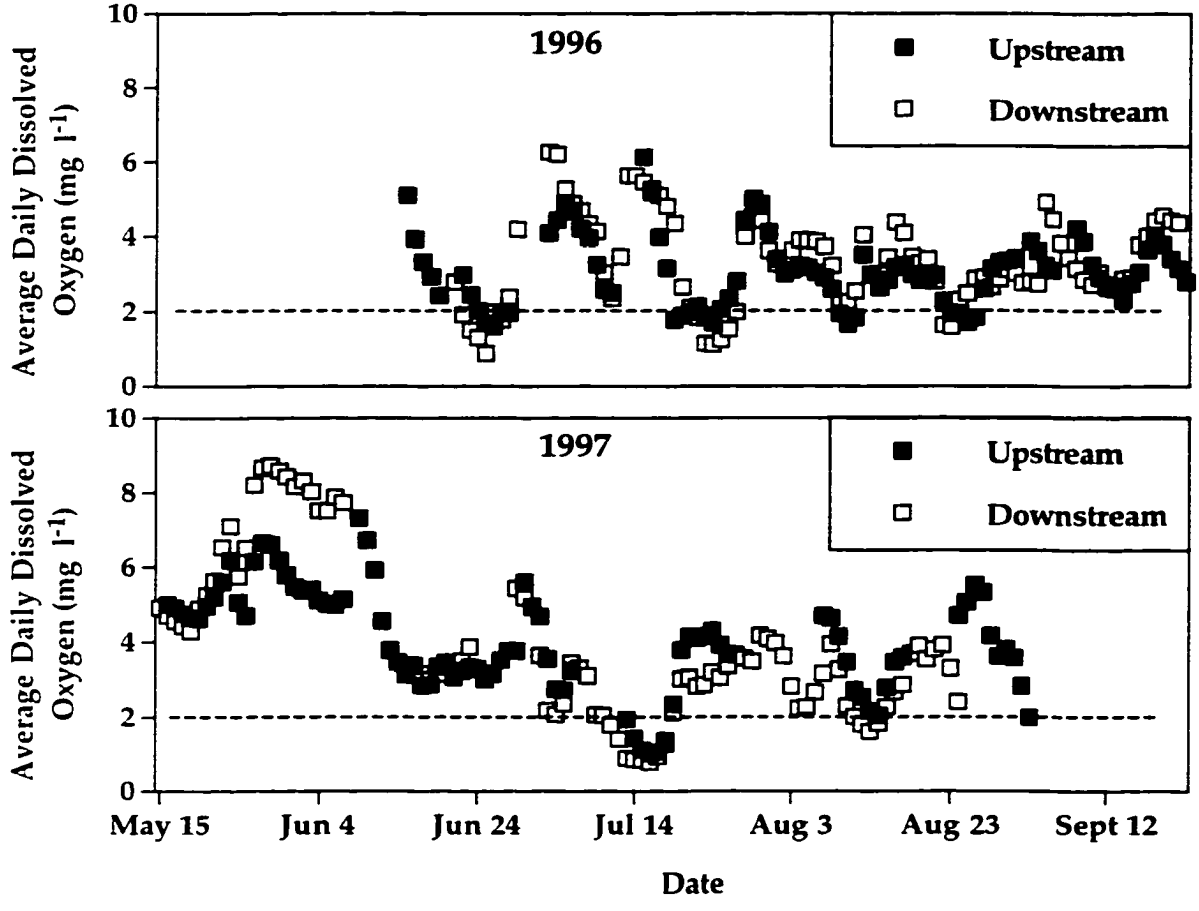


Fig. 4. Hourly dissolved oxygen concentrations for upstream and downstream areas during two hypoxic episodes: June 22 - June 28, 1996 and July 14 - July 20, 1997.

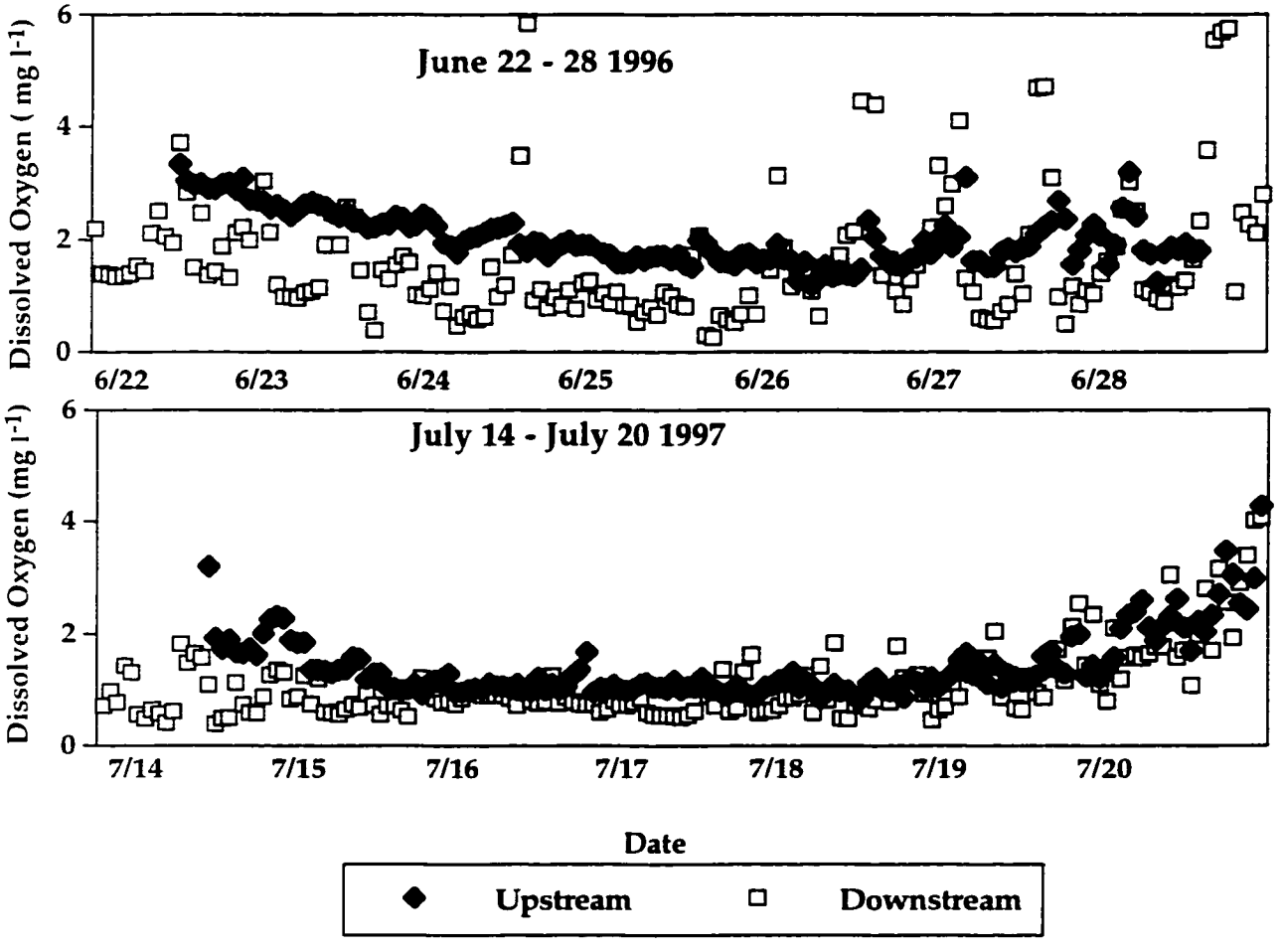


Fig. 5. Daily temperature and salinity for upstream and downstream areas in 1996 and 1997. We averaged hourly measurements to provide daily averages.

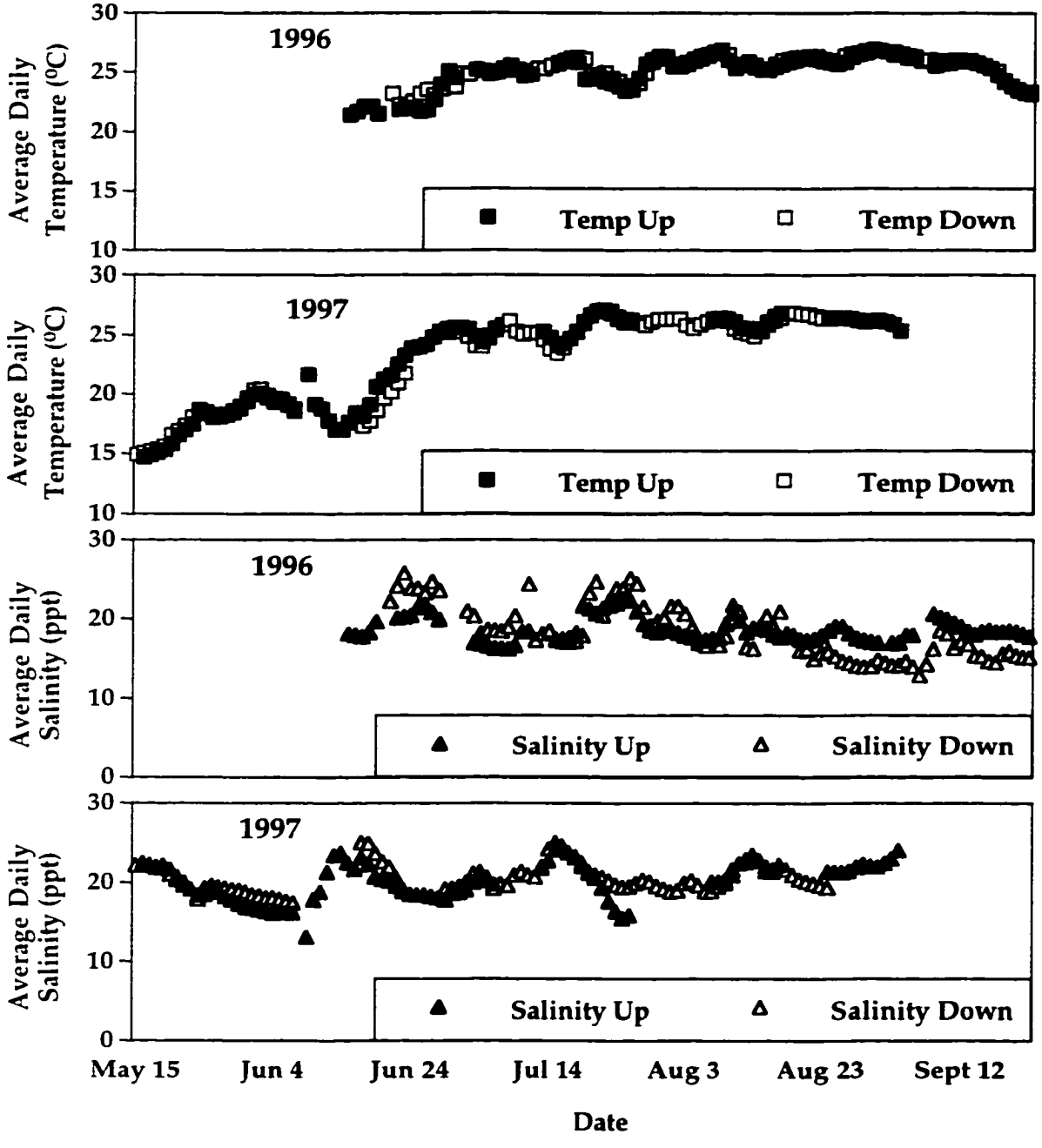


Fig. 6. Species richness (mean ± 1 standard error) of epifauna from upstream and downstream areas in 1996 and 1997.

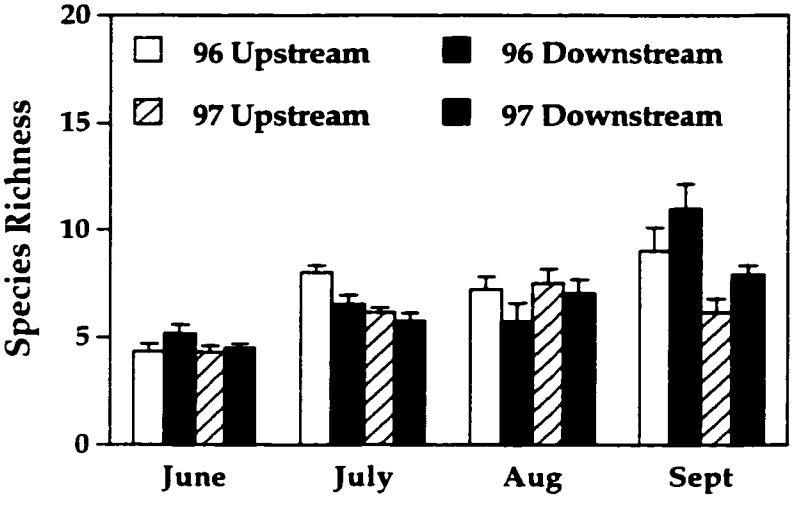


Fig. 7. Percent cover (mean ± 1 standard error) of sessile epifaunal species that covered at least 5% of panels from upstream and downstream areas at some point during the summer of 1996 (a) and 1997 (b). Some error bars are difficult to see because standard errors for some species were small.

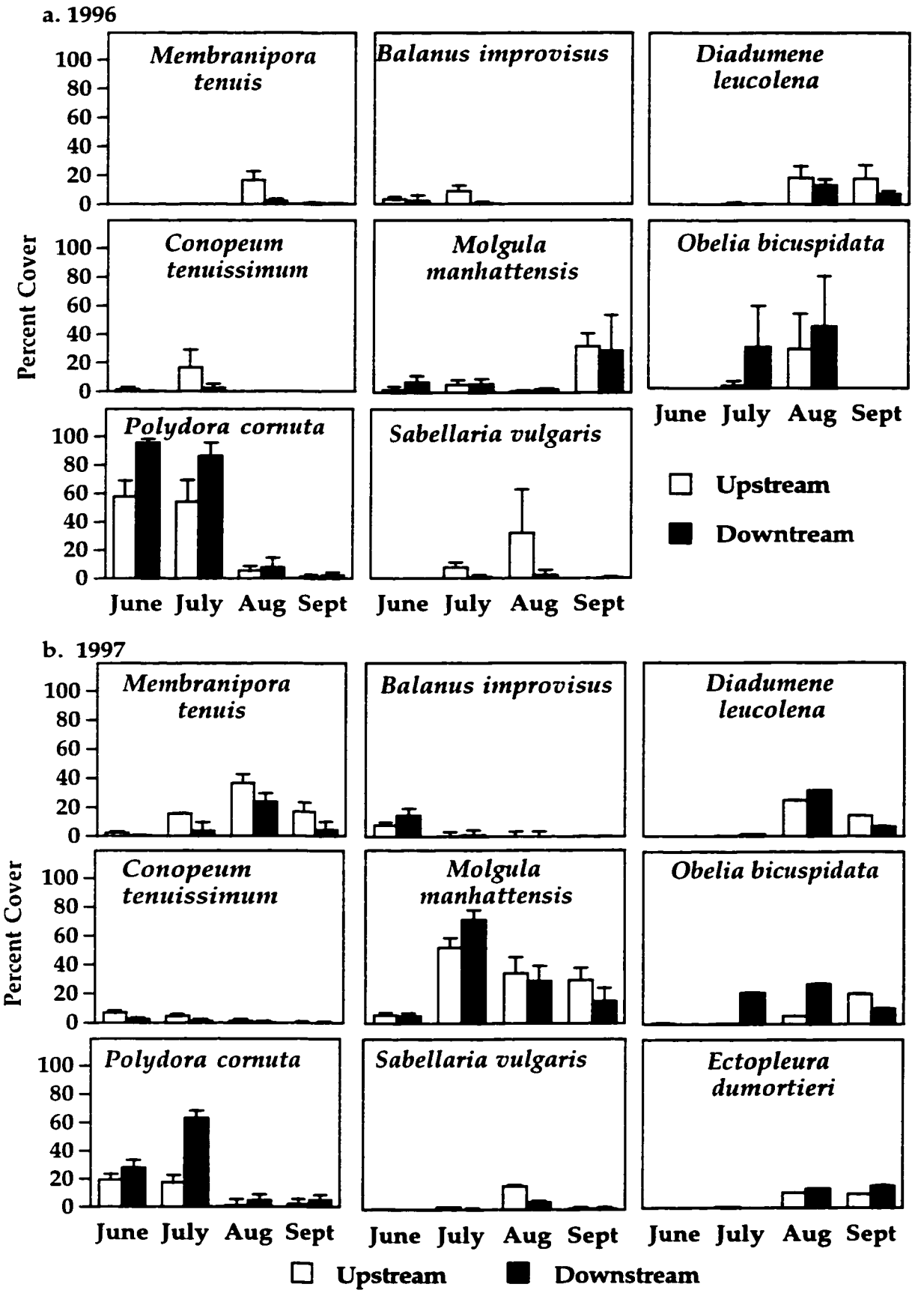


Fig. 8. Abundance (mean per panel ± 1 standard error) of mobile species that were common in the summer of 1996 (a) and 1997 (b). Note variation in scales.

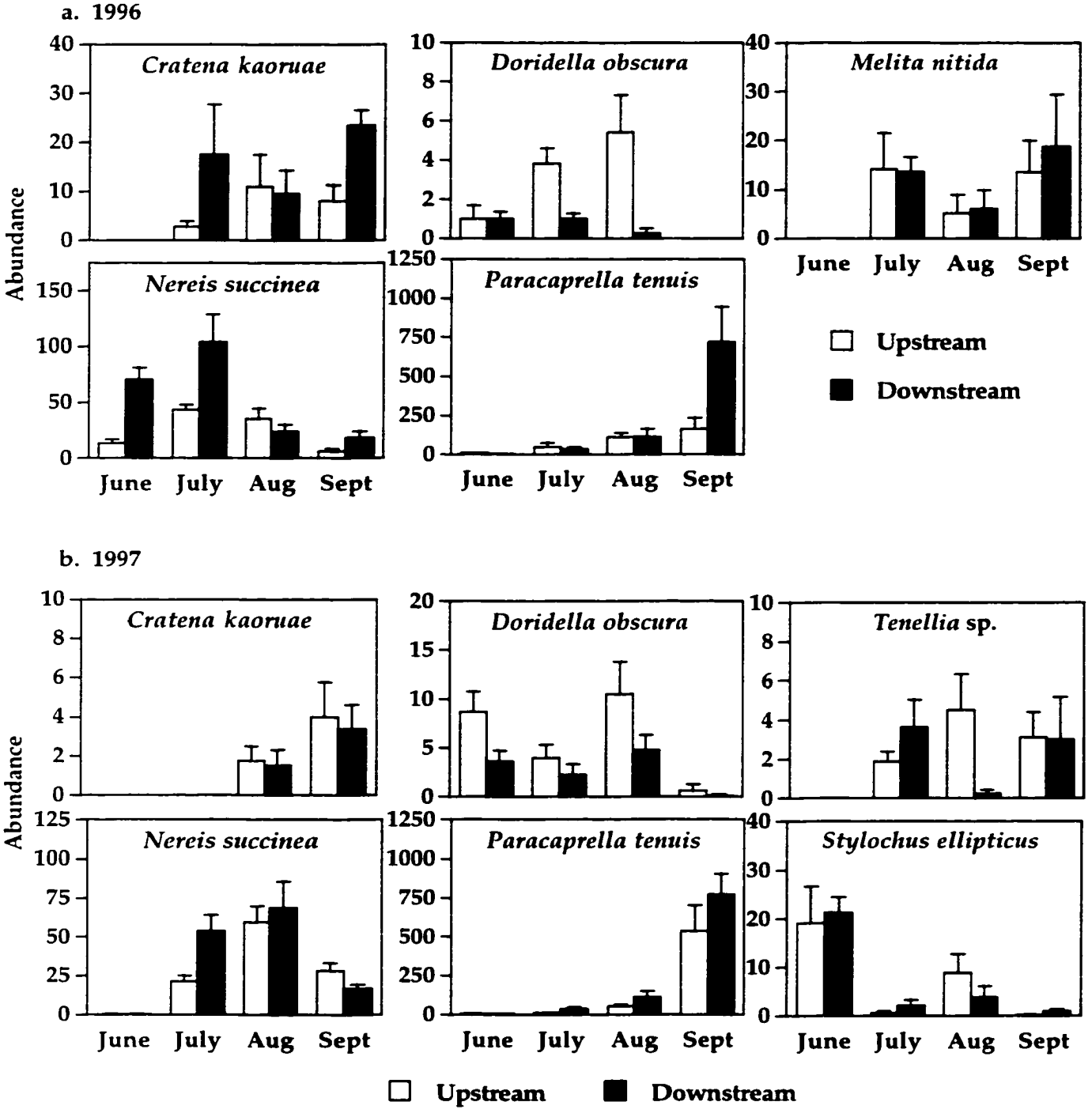
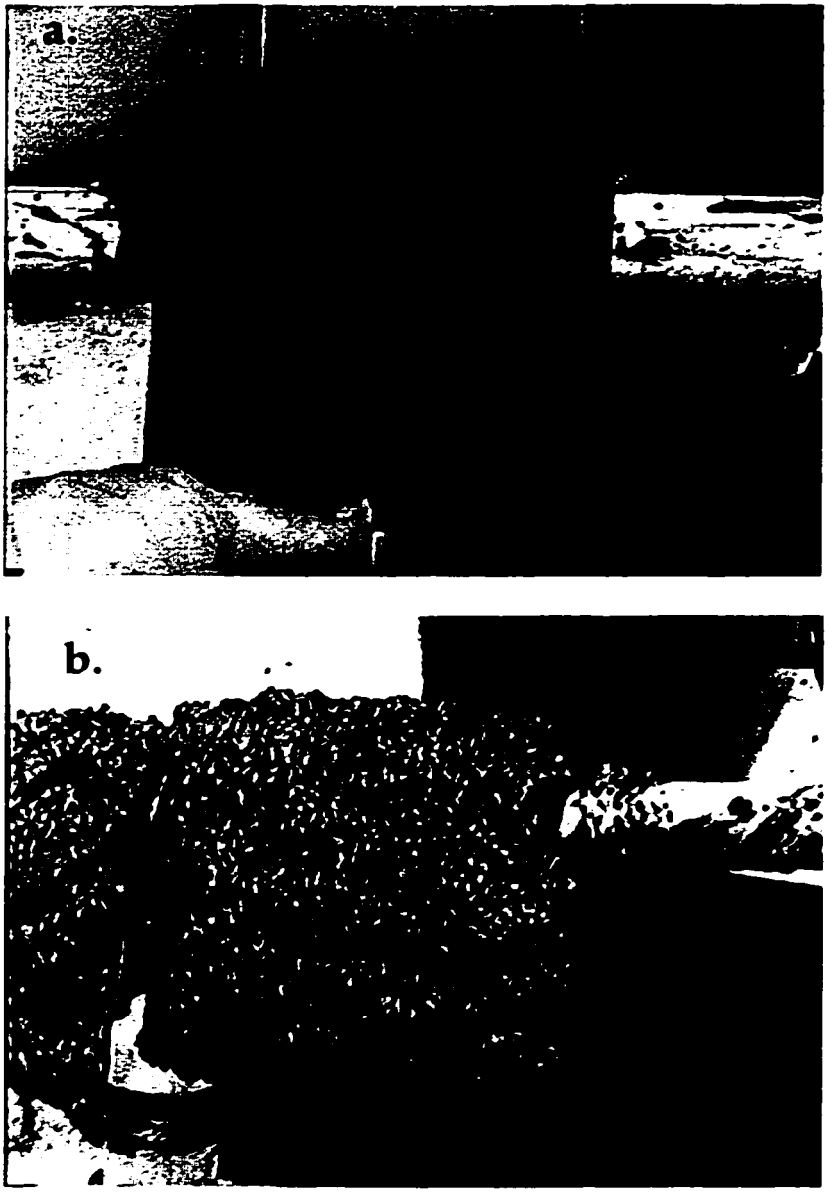


Fig. 9.

a. A clean panel before deployment.

b. A panel exposed for 1 month, showing rapid growth of *Polydora cornuta* tubes.



Appendix 1. Deployment dates in 1996 and 1997, as well as dates during each deployment when daily average oxygen concentrations fell below 2 mg O_2 / L.

Deployment	Date deployed	Date retrieved	Dates with average oxygen concentrations < 2 mg O_2 / L
June 1996	5/20/96	6/20/96	6/19
July 1996	6/22/96	7/22/96	6/22 - 6/28
August 1996	7/24/96	8/21/96	7/24 - 7/27
September 1996	8/23/96	9/23/96	8/23 - 8/26
June 1997	5/17/97	6/18/97	
July 1997	6/18/97	7/16/97	7/12 - 7/16
August 1997	7/16/97	8/14/97	7/16 - 7/19, 8/13-8/14
September 1997	8/14/97	9/12/97	8/14 - 8/16

CHAPTER 2: EFFECTS OF PERIODIC HYPOXIA ON MORTALITY, FEEDING AND PREDATION IN AN ESTUARINE EPIFAUNAL COMMUNITY.

Abstract

Stress tolerance among species can influence community organization by altering the probability of disturbance and the outcome of species interactions. The York River Estuary, a tributary of the Chesapeake Bay, USA, experiences periodic low oxygen stress (hypoxia), yet epifaunal species form dense communities there. We studied hypoxia tolerance of common epifaunal species in the York River by exposing sessile and mobile epifauna to high and low oxygen concentrations in laboratory aquaria. Mortality in hypoxia varied among species, ranging from 0-100%, with trends of decreased tolerance by mobile species relative to sessile species. Many species had a median lethal time (LT_{50}) in hypoxia greater than 1 week (3 of 6 species at 1 mg O_2 / L and 6 of 14 species at 0.5 mg O_2 / L), the maximum duration of typical hypoxic episodes in the York River, suggesting that hypoxia may cause little mortality for many species in this system. However, hypoxia had sub-lethal effects on behavior in all species tested. Epifaunal animals responded to hypoxia with behaviors that moved them higher in the water column or by entering resting states until hypoxia passed. Feeding and predation by a variety of taxa (the hydroid *Obelia bicuspidata*, the mud crab *Neopanope sayi*, juvenile blue crabs *Callinectes sapidus*, the flatworm *Stylochus ellipticus*, and the nudibranch *Doridella leucolena*) decreased during hypoxia, despite varying mortality responses to low oxygen stress, suggesting that short hypoxic episodes may create predation refuges for prey species. At least one highly tolerant species (*O. bicuspidata*) showed substantially decreased growth in hypoxia. Although high tolerance of hypoxia by estuarine epifauna limits serious disturbance during

brief hypoxic episodes, hypoxia's greatest impact on York River epifaunal communities might be through its indirect effects on behavior and predation.

Introduction

The tolerance of stress by a species can influence its distribution and abundance (Sousa 1979, Grossman et al. 1998) by changing the likelihood of disturbance (Sousa 1984, Connell et al. 1997), the rate of population growth (Huston 1979, Huston 1994) and the outcome of interactions with other species (Menge 1978, Witman and Grange 1998). Species that lack adaptations for surviving stresses often are excluded from stressed areas, leading to low diversity communities dominated by fewer, highly tolerant species (Menge and Sutherland 1987). Stress can also decrease the abundance of intolerant species through sub-lethal effects that disrupt normal behaviors and activities, leading to decreased rates of population growth (Huston 1994). In addition, the relative stress tolerance of different species in a community influences interactions among those species, further altering stressed communities (Breitburg et al. 1994). For example, many predators on rocky intertidal shores are less tolerant of physical stress from waves than their prey, leading to decreased predation in high wave environments and allowing prey to use stressed areas as predation refuges (Menge and Sutherland 1987). Other physiological stresses such as pollution may affect all trophic levels similarly, leading to few changes in predation pressure with increasing stress (Menge and Olson 1990).

In some aquatic communities, benthic invertebrates experience stress from low oxygen, termed hypoxia. Dissolved oxygen concentrations in the water column of 2 mg O_2 / L or lower often have deleterious effects on animals and are considered hypoxic (Tyson and Pearson 1991). Hypoxia occurs worldwide in lakes, estuaries and coastal areas (Diaz and Rosenberg 1995) when density stratification prevents atmospheric oxygen from mixing into sub-pycnocline water, and respiration depletes dissolved oxygen below the pycnocline (Officer et al. 1984). In many systems, anthropogenic eutrophication is increasing the frequency and duration of hypoxia by increasing microbial respiration (Diaz and Rosenberg 1995).

The effects of hypoxia on biotic communities depend in part on its severity (how low dissolved oxygen concentrations fall) and duration. In extreme cases, where hypoxia lasts for many weeks or approaches anoxia (a complete lack of dissolved oxygen), hypoxia can cause emigration of mobile animals (Diaz and Rosenberg 1995) and mass mortality of sessile animals (Jørgensen 1980, Stachowitsch 1984). When oxygen conditions are milder (dissolved oxygen concentrations remain well above anoxic levels) or hypoxic episodes are brief, hypoxia can change species composition (Josefson and Widbom 1988, Llanso 1992) and reduce benthic biomass (Dauer et al. 1992).

Animals have many physiological and behavioral methods for tolerating hypoxia, which vary depending on the duration and severity of hypoxia (Hagerman 1998). During mild hypoxia (oxygen concentrations remain well above anoxia) or brief hypoxic episodes (hours to days), many animals enhance aerobic metabolism with behaviors that increase the flux of oxygen to their bodies (Hagerman 1998). Mobile species swim toward higher oxygen areas (Das and Stickle 1994, Hagerman and Vismann 1995, Cochran and Burnett 1996), and infaunal species crawl to the sediment surface where oxygen is higher than in the sediments (Rosenberg et al. 1991, Nilsson 1999). Animals may increase ventilation rates of gills (Kramer 1987) and increase ventilation of tubes and burrows (Gerhardt and Baden 1998). In addition, some invertebrates can increase the oxygen affinity of their blood pigments (Mangum 1970, deFur et al. 1990).

When oxygen concentrations approach anoxia or hypoxic episodes are long-lasting (days to weeks), tolerant animals survive by using large energy stores (Hochachka et al. 1973, Arndt and Schiedek 1997), decreasing metabolic rates and using anaerobic metabolism (Hochachka and Somero 1984, Hagerman 1998). To reduce metabolic rates, animals become quiescent (Gerhardt and Baden 1998, Nilsson 1999), reduce growth (Forbes and Lopez 1990, Nilsson 1999) and delay reproduction (Eriksson and Weeks 1994, Vopel et al. 1998). Many invertebrates can use relatively efficient anaerobic pathways

(Hagerman 1998), and some animals can vary anaerobic pathways depending on the oxygen level (Arndt and Schiedek 1997).

Animals in severely hypoxic or anoxic environments may also need adaptations to survive high sulfide concentrations (Theede et al. 1969) and hypercapnia, the presence of high concentrations of CO_2 (Burnett 1997), which are associated with low oxygen. Sulfide decreases survival during hypoxia (Hagerman and Vismann 1995, Vistisen and Vismann 1997) and makes recovery from hypoxia more difficult (Vismann and Hagerman 1996). For a wide variety of taxa, species with high tolerance to hypoxia also have high tolerance to sulfide (Theede et al. 1969, Hagerman 1998). Hypercapnia reduces pH and may also decrease survival during hypoxia, but many taxonomic groups have adaptations that buffer internal pH (Burnett 1997).

Tolerance to hypoxia varies among taxonomic groups and can help determine species distributions (McMahon and Russel-Hunter 1978, Marshall and McQuaid 1993, Nielsen and Hagerman 1998). Phylogenetic groups with complex structures that insulate respiring tissue from the environment are generally less tolerant of hypoxia than groups where the respiring tissue remains in close contact with the surrounding water (Mangum and van Winkle 1973). Polychaetes, bivalves, platyhelminths and cnidarians are relatively tolerant, while crustaceans and vertebrates have relatively low hypoxia tolerance (Mangum and van Winkle 1973; Diaz and Rosenberg 1995).

Hypoxia tolerance may also vary among habitats, with animals from habitats that often experience low oxygen being more tolerant than animals less likely to encounter hypoxia (Theede et al. 1969, Sassaman and Mangum 1972, Vistisen and Vismann 1997). Some studies suggest that infaunal species, which live within the sediment, tolerate hypoxic stress better than epifaunal species, which live on the sediment surface (Hagerman 1998). For example, authors have compared the hypoxia tolerance of infaunal and epifaunal species of anemones (Sassaman and Mangum 1972), brittle stars (Vistisen and Vismann 1997), snails (McMahon and Russell-Hunter 1978) and polychaetes (Theede et al. 1973) and

found that infaunal species were more tolerant in each case. However, some epifaunal groups are abundant in areas with low oxygen, suggesting that these species may be highly tolerant of hypoxia (Tunnicliffe 1981; Sagasti et al. in press). The tolerance of hypoxia by many epifaunal groups (such as hydroids and bryozoans) is unknown.

In addition to killing animals directly, hypoxia can change behavior (Hagerman 1998), feeding rates, growth (Forbes and Lopez 1990) and the outcome of species interactions, including predation (Breitburg et al. 1994, Nestlerode and Diaz 1998, Legeay and Massabuau 2000). Many species respond to hypoxia with behaviors that help them stretch higher into the water column where oxygen concentrations are generally higher (Hagerman 1998, Diaz and Rosenberg 1995). Hypoxia depresses feeding in some species (Sobral and Widdows 1997, Rosas et al. 1998) while increasing it in others (Breitburg et al. 1994). Reduced feeding by fishes (Kramer 1987), shrimp (Rosas et al. 1998) and bivalves (Sobral and Widdows 1997) may help these species survive by decreasing metabolic costs, but reduced feeding can also decrease growth (Forbes and Lopez 1990, Rosas et al. 1998). In contrast, some predators can increase feeding rates during hypoxia because their prey's defenses decrease (Kramer 1987, Norkko and Bondsdorf 1995, Nestlerode and Diaz 1998). The relative tolerance of predators versus prey may determine whether predation rates increase or decrease during hypoxia (Breitburg et al. 1994). For example, predation on larval fish by jellyfish can increase during hypoxic episodes, because jellyfish tolerate hypoxia, but larval fish are unable to evade predators in low oxygen (Breitburg et al. 1994). Concurrently, predation on larval fish by adult fish decreases, because the adult fish are intolerant of hypoxia (Breitburg et al. 1994). Some predators switch prey species as oxygen falls, preferring to exploit the most intolerant prey (Sandberg 1994). In areas with fluctuating oxygen levels, mobile predators can temporarily leave hypoxic areas, then return when oxygen rises to take advantage of infaunal invertebrates that surface during low-oxygen events (Pihl et al. 1992; Rahel and Nutzman 1994, Nestlerode and Diaz 1998).

Epifaunal animals such as barnacles, anemones, hydroids, and tunicates are abundant in the York River Estuary, Chesapeake Bay, USA (Schaffner et al. in press) despite frequent hypoxia (Kuo and Neilson 1987). Epifaunal species in the Chesapeake Bay have highly seasonal distributions and are most abundant in the summer (Abbe 1987; Sagasti et al. in press), which is also when hypoxia occurs (Kuo and Neilson 1987). In the York River, oxygen concentrations follow relatively predictable cycles, with hypoxia occurring in June - September during neap tides and disappearing during spring tides (Haas 1977). Hypoxic episodes last from several days up to a week, with typical duration of 5 days (Kuo et al. 1993). Epifaunal communities in the York River have similar species composition in deep areas where hypoxia is common and in shallow areas where hypoxia does not occur (Sagasti et al. in press). In addition, species abundance is similar throughout the lower York River (Sagasti et al. in press), even though some areas experience lower oxygen concentrations than others (Sisson et al. 1991, Sagasti et al. in press). This suggests that epifaunal species characteristic of the York River may be resistant to periodic hypoxia.

Species interactions such as predation may be important for structuring epifaunal communities in the Chesapeake Bay (Branscomb 1976, Marsh 1976, Rheinhardt and Mann 1990), and hypoxia could change these interactions (Breitburg et al. 1994). Major predators on epifaunal species in the Chesapeake Bay include fish, crabs (Rheinhardt and Mann 1990), flatworms (Branscomb 1976), snails and nudibranchs (Marsh 1976). Large crabs and fish leave low-oxygen areas during hypoxic episodes, but may return after these episodes to feed on stressed prey items (Pihl et al. 1992; Nestlerode and Diaz 1998). Small predators such as mud crabs and juvenile blue crabs belong to a relatively intolerant phylogenetic group (i.e.. crustaceans, Gerhardt and Baden 1998) and may be too small to escape hypoxic areas; therefore, their predation rates might decrease during hypoxia. Other small predators such as flatworms and snails belong to relatively tolerant phylogenetic

groups (McMahon and Russell-Hunter 1978; Armonies 1986) and might increase feeding rates if hypoxia makes their prey more vulnerable.

This study examined the hypoxia tolerance in epifaunal species of the York River Estuary. We considered the effects of hypoxia on mortality, behavior, feeding rates and predation. For the most abundant epifaunal species in the York River Estuary, we calculated the median lethal time (LT_{50}) at two oxygen concentrations (1 mg O_2 / L and 0.5 mg O_2 / L) common in the York River during hypoxic episodes to determine whether tolerance varies among species and whether short hypoxic episodes at these oxygen concentrations could cause widespread mortality. We also investigated the effects of hypoxia on feeding by a highly tolerant sessile species and on predation by the most abundant small, mobile predators in this system to determine if hypoxia changes feeding rates and if prey might use hypoxic areas as predation refuges. Finally, we relate the tolerance of individual species to their abundance in hypoxic areas to examine whether hypoxia could influence the distribution of epifaunal species in this system.

Methods

Collection of epifauna

We tested the hypoxia tolerance of dominant epifaunal species in the York River, Chesapeake Bay, USA during the summer when hypoxia occurs (Kuo and Neilson 1987). We collected 8 of the 9 most common sessile species, as determined during a previous study in this system (Sagasti et al. in press). We also collected 7 mobile species, 6 of which were abundant during the previous study (Sagasti et al. in press) and one (juvenile blue crab *Callinectes sapidus*) which has been found by others to be an important predator in Chesapeake Bay epifaunal communities (Rheinhardt and Mann 1990). Sessile species were collected by submersing 10 X 10 cm PVC panels or 2.6 X 7.6 cm glass microscope slides from the Virginia Institute of Marine Science (VIMS) pier in the York River at a depth of 1-

2 m and allowing epifaunal animals to colonize. We collected species after panels or slides had been immersed less than 3 weeks to ensure that populations were young and actively growing. The tube-building polychaete *Sabellaria vulgaris* was collected on empty shells of the clam *Mercenaria mercenaria* under the VIMS pier. Epifaunal species in the York River have highly seasonal recruitment periods (Sagasti et al. in prep.), so we repeated the collection process several times each summer in 1997-1999 to maximize the diversity of collected species.

On each substratum, we removed all but one species. For most species, we left only one animal or colony on each substratum, but for a few species we left multiple animals on each substratum (Table 1), ensuring that individuals did not touch each other. It was difficult to distinguish among colonies of the hydroid *Obelia bicuspidata*, so all animals were removed except for a 1 cm^2 area of hydroid (Table 1). The polychaete *Polydora cornuta* builds U-shaped mud tubes that are entwined together, making it difficult to isolate a single individual, so we left intact a 1 cm^2 area covered with *P. cornuta* tubes (Table 1).

Mobile species were collected by hand from the VIMS pier, except for juvenile blue crabs (*Callinectes sapidus*) which were collected with dip nets in 1-2 m deep eelgrass beds off Goodwin Island (York River, approximately 7 km from VIMS). Mobile animals were placed in one of 2 cage types, termed "large cages" and "small cages" (Fig. 1). We kept blue crabs and mud crabs (*Neopanope sayi*) in 11 X 11 X 7 cm cages with 1 mm mesh plastic window screening on 5 sides and a solid plastic back on the sixth side (large cages). Smaller animals were kept in finger bowls (5.5 cm diameter, 2.3 cm height) covered on top by 125 μm nytex mesh (small cages). In one experiment (15-20 August 1999) we put mud crabs in small cages with 1 mm mesh rather than 125 μm mesh. We held animals in aquaria with flow-through York River water for 1-3 days before using them in experiments.

Experimental design

In the summers of 1997-1999, we conducted a series of laboratory experiments exposing epifaunal species to high and low oxygen conditions (Table 1). Due to logistical constraints, up to 4 species shared aquaria in some experiments. However, strong inter-species effects appear unlikely because different species had no physical contact, they shared a water volume much larger than their body volumes, they were fed in excess, and all dead animals were removed immediately.

For each species, we randomly assigned one substratum or cage containing animals to randomly interspersed control (high-oxygen) and experimental (low-oxygen) 40 L aquaria. Each treatment (high and low oxygen) had 5 (7 - 12 June 1997), 8 (all remaining experiments in 1997) or 10 (1998-1999) replicate aquaria. Within each aquarium, substrata with sessile epifauna were hung along the sides of aquaria, with animals facing towards the middle of each aquarium (Fig. 1). Large cages were placed with the solid side against the sides of aquaria, and mesh sides facing towards the middle (Fig. 1). Small cages were placed on the bottom of aquaria with the mesh on top (Fig. 1).

Each aquarium was filled with sea water pumped from the VIMS pier and passed through two sand filters to remove animals and debris. Salinity in the York River near VIMS changes predictably each year (Sagasti et al. in press), rising steadily from spring until fall. Therefore, experiments conducted in June-July each year had salinities of 16-18 ppt, and experiments in August or September had salinities of up to 23 ppt. Experiments were conducted at room temperature (20-26 ^{o}C), similar to the temperature range in the York River during summer (Sagasti et al. in press). Aquaria were kept in the dark to mimic deep areas of the York River where hypoxia occurs. To prevent hypercapnia and maintain normal pH (Burnett 1997), 300-500 ml oyster shell hash buffered the pH in each tank (Fig. 1). Currents in the York River during hypoxia can reach 40 cm / s (Sisson et al. 1991), so submersible pumps in each aquarium maintained recirculating water flow of 400 L / hr (1997) or 580 L / hr (1998-1999). Each pump was connected to a 2.5 cm diameter plastic

hose that ran down the center along the length of each aquarium (Fig. 1); water flowing through small holes spaced every 2.5 cm along the hose created relatively uniform water flow throughout each aquarium.

To ensure that water mixed throughout aquaria and flowed easily in and out of cages, we used dye tracers to examine water movement. Dye injected anywhere within an aquarium dispersed throughout the aquarium within 5-10 seconds, suggesting that oxygen concentrations were relatively homogenous throughout aquaria. Similarly, dye injected in large cages completely dispersed out of cages in 5-10 seconds, suggesting that oxygen concentrations were likely to be similar inside and outside large cages. Dye in small cages showed a different pattern; dye in the upper half of the cages dispersed quickly around the aquaria (< 30 seconds), but dye in the bottom half remained stagnant. These results suggested that small cages had strong flow at the top but not the bottom. However, we believe animals in small cages experienced relatively similar oxygen conditions to those in the rest of the tanks for three reasons. First, animals in hypoxia usually clung to the top of cages where they would have experienced relatively high mixing with the rest of the tank. Second, animals in these cages were small so they could not have respired at a sufficiently high rate to change oxygen conditions drastically. Third, in 1999 we compared the mortality in small cages vs. a new set of cages (called "new cages"), with the same mesh size but different design. We made new cages using PVC pipe (2.5 cm inside diameter, 2.5 cm long), with 125 μm nytex mesh covering both ends. Dye in new cages dispersed into the rest of the tank within 10 seconds. In experiments with the polychaete *Nereis succinea*, we used half new cages and half old small cages. We observed nearly identical mortality in both cage-types (21-26 June 1999: 4 of 5 *N. succinea* died in small cages, 4 of 5 died in new cages; 15-20 August 1999: 4 of 5 *N. succinea* died in small cages, 3 of 5 died in new cages).

After placing animals in aquaria, we bubbled high-oxygen tanks with air to maintain oxygen concentrations above 4 mg O_2 / L; low-oxygen tanks were bubbled with a

combination of air and N_2 gas to achieve target oxygen concentrations (1 mg O_2 / L in 1997: 0.5 mg O_2 / L in 1998 and 1999) during the first 6 hours of each experiment, a period over which similarly abrupt oxygen changes take place in the York River (Kuo and Nielson 1987). Plastic wrap over the surface of each aquarium limited contact with the atmosphere. Oxygen and temperature in each aquarium were measured 6-10 times each day using a YSI model 38 oxygen monitor, calibrated daily. When oxygen differed from the target concentration, we changed the proportions of air and N_2 to correct the concentration. After 5 days, a typical duration for hypoxia in the York River (Kuo and Nielson 1987), oxygen in low-oxygen aquaria was raised to > 4 mg O_2 / L to let animals revive. Before raising oxygen, we measured the pH in each aquarium using a Beckman Φ220 pH meter or a Corning pH/ion analyzer 350.

To prevent the build-up of metabolic byproducts, each day we removed 20% of the water volume of each aquarium and replaced it by siphoning water from one of two randomly selected, oyster-shell buffered reserve tanks. Reserve tanks were filled with York River water and oxygen concentrations in each tank were decreased to < 1 mg O_2 / L by bubbling with N_2 gas. After replacing water in low-oxygen tanks, we increased oxygen in the reserve tanks to > 3 mg O_2 / L by bubbling with air and subsequently replaced water in high-oxygen tanks. Thus, all tanks used water that differed only in oxygen concentration.

Each species was fed an appropriate diet (Table 1). We fed suspension feeders a variety of foods (Table 1) including liquid filter feeder food (Liquefy Marine, from Interpet, 5 drops / aquarium daily), feeding blocks that dissolved over time (Reefcare Invertebrate Feeding Blocks, 0.5 block / aquarium, dissolved over the course of each experiment), algae paste (diatom *Thalassiosira weissflogii*, approximately 0.5 X 10^8 cells per tank daily), brine shrimp (*Artemia* sp., < 6 hours after hatching), or plankton (variable concentrations caught with a plankton net on the VIMS pier). Predators were offered epifaunal animals collected on the VIMS pier (Table 1). For most experiments, we placed predators and prey together in aquaria at the beginning of experiments so that both species experienced similar oxygen

conditions throughout the experiment as they would in the natural environment. During two experiments with mud crabs *Neopanope sayi* (7-12 June 1997; 23-28 June 1997), we placed predators and prey together in aquaria at the beginning of the experiment, then removed remaining prey items and added new ones after two and three days respectively. Two species (the worm *Nereis succinea* and the snail *Mitrella lunata*) were not fed because we could not provide an appropriate diet.

We observed all animals daily to determine if they were alive, using appropriate criteria for each species (Table 1), and removed dead animals. When possible, we observed animals without disturbing them. For a few species, it was necessary to observe animals using dissecting microscopes. In these cases, animals were placed in dishes with water from their own aquarium; to prevent oxygen from changing, we observed the animals quickly without jostling dishes. In all cases it took less than 10 minutes to observe animals and return them to aquaria. In experiments with *Polydora cornuta*, we observed a 0.5 cm^2 section, and counted tubes and the number of worms inside the tubes. During 1998 experiments with the bryozoan *Membranipora tenuis*, we observed 30 zooids starting from the center of each colony and moving outward. In 1999 experiments with the bryozoans *M. tenuis* and *Conopeum tenuissimum*, we placed colonies under a grid and observed 10 random zooids. We placed the hydroid *Obelia bicuspidata* beneath a grid and, using a dissecting microscope, observed the number of hydranths on 10 random upright stems. Some colonies lost all hydranths; we could not determine if these colonies were alive until after the experiment, when they were placed in high oxygen and observed for new growth.

Feeding and predation

To examine the sub-lethal effect of hypoxia on feeding and predation, we observed species that ranged from highly tolerant (*Obelia bicuspidata*) to relatively intolerant (mud crabs, blue crab juveniles) of hypoxia and which included many of the most common small predators on epifaunal species (Sagasti et al. in press). We fed the hydroid *Obelia*

bicuspidata a combination of brine shrimp and zooplankton (Table 1) dyed orange with non-toxic Eosin Y dye. Fifteen minutes after feeding each colony, we observed it using a dissecting microscope, placing colonies under a grid and observing 10 randomly selected upright stems. For each stem, we counted the number of hydranths and whether they had eaten (orange prey were visible through hydranths). For experiments with predators (mud crabs *Neopanope sayi*, blue crab juveniles *Callinectes sapidus*, flatworms *Stylochus ellipticus*, and nudibranchs *Doridella obscura*) it was important to distinguish between prey that were eaten and those that died from low-oxygen. For mud crabs feeding on the polychaete *Nereis succinea* (Table 1), the worm was considered eaten if it was missing from the cage. We fed barnacles *Balanus improvisus* to blue crabs, mud crabs and flatworms (Table 1). When barnacles died from hypoxia, they turned black within their shells but remained intact. When they were eaten by crabs, the shells were broken and empty. When barnacles were eaten by flatworms, the shells were intact but empty. For the nudibranch *Doridella obscura* preying on the bryozoan *Membranipora tenuis* (24-29 August 1997), each aquarium had one cage with only bryozoans (predator excluded) and a second cage with bryozoans plus nudibranchs (predator present). On the third day of this experiment, we counted all bryozoan zooids that were healthy, that had died intact, or that were empty. All cages without predators had fewer than 2% empty zooids, while those with predators had up to 66% empty zooids; thus, we assume that most empty zooids were eaten.

Predation during vs. following hypoxia

It is possible that even if predators decrease feeding rates during low oxygen, they may compensate by increasing feeding rates when oxygen increases such that the prey species derives no net benefit from a low-oxygen predation refuge. To determine whether prey species could benefit from decreased feeding during hypoxia, we examined an extreme case with a relatively intolerant predator (mud crab *Neopanope sayi*) and a relatively tolerant prey species (barnacle *Balanus improvisus*), because in this scenario the use of hypoxia as

a predation refuge would be most likely. The experiment was similar to those described above, except that plastic containers (10 X 10 X 6.3 cm) were used instead of aquaria, and low oxygen concentrations (target 1 mg O_2 / L) were only maintained for 2 days, after which oxygen was increased to > 5 mg O_2 / L in all containers for an additional 3 days. In each container we placed one crab (8-15 mm carapace width) and 20 barnacles (2-4 mm basal diameter). Barnacles were fed with liquid filter feeder food (Liquefy Marine, from Interpet, 1 drop / container daily), and each day we determined whether barnacles were living, dead, or eaten.

Statistical analysis

For each species with greater than 1% mortality in low oxygen we calculated the median lethal time (LT_{50}) in hypoxia using maximum likelihood normit analysis (Newman 1995). For each species, the cumulative proportion of animals that died in low-oxygen treatments each day was used in the analysis. When species had more than one animal per aquarium we calculated the proportion dead and used this proportion to calculate the overall proportion dead in hypoxic aquaria. We used Pearson Chi-squared goodness-of-fit tests to determine if models fit the data for each species, and in all cases the data adequately fit the models (Newman 1995). However, for species with little mortality during experiments, models could not predict 95% confidence intervals. For this reason, we could not provide confidence intervals for species with LT_{50} greater than 5 days. For species with less than 1% mortality in low oxygen, we did not calculate LT_{50}s but instead determined that they were highly tolerant.

To determine if oxygen affects feeding and predation, we used a variety of analyses to compare feeding and predation in high- vs. low-oxygen treatments. For the hydroid *Obelia bicuspidata*, repeated measures ANOVAs compared the number of hydranths per stem, and the percentage of hydranths that fed each day, in high vs. low oxygen conditions. Because hydroids feed with their hydranths, the number of hydranths per stem is a measure

of colony feeding potential. The percentage of hydranths that fed is a more direct measure of whether individual polyps fed. For each analysis, assumptions of parametric statistics were checked using Cochran's test for homogeneity of variance (Underwood 1997) and the Shapiro-Wilkes test for normality (Zar 1996). To meet assumptions for the number of hydranths per stem, we transformed data using log (x+1). The percentage of stems that fed were normally distributed and had homogenous variances, so these data were not transformed.

To determine if oxygen changed predation by common small predators, we used Mann-Whitney U-tests to compare the number of prey eaten by living predators in high vs. low oxygen. Because we only included data from living predators, sample sizes differed between treatments. For experiments with mud crabs *Neopanope sayi* preying on the polychaete *Nereis succinea* (7-12 June 1997) or the barnacle *Balanus improvisus* (23-28 June 1997), we compared the number of prey eaten by crabs at the end of each feeding period (days 0-1 and 2-4 for *N. succinea*, days 0-3 and 4-5 for barnacles). In experiments with the flatworm *Stylochus ellipticus* preying on the barnacle *Balanus improvisus* (23-28 June 1997), there was high mortality of flatworms, and there were two flatworms present in each cage. To have sufficient sample sizes and to minimize effects of flatworms that died on remaining flatworms, we compared only the cumulative number of barnacles eaten in high vs. low oxygen on days 0-2 by flatworms in cages where both flatworms survived. However, the trends we saw during the first two days continued for the rest of the experiment. For the nudibranch *Doridella obscura* preying on the bryozoan *Membranipora tenuis*, we calculated predator effect by subtracting the percent of zooids that were empty in predator excluded cages from the percent empty with the predator present. Finally, we compared predator effect in high vs. low oxygen, considering only aquaria where the nudibranch survived until the third day of the experiment. In experiments with blue crab juveniles (*Callinectes sapidus*) preying on barnacles *Balanus improvisus* (19-25 July 1998), we had high mortality of blue crabs, so we only considered feeding

during the first three days, when many crabs were still alive. We compared the cumulative number of barnacles eaten in high vs. low oxygen on days 1-3 by crabs that survived until day 3.

To examine predation by mud crabs *Neopanope sayi* on barnacles *Balanus improvisus* during vs. following hypoxia, repeated measures ANOVA related the number of barnacles eaten per day to oxygen treatment (low vs. high) and time (during vs. following hypoxia). Assumptions of parametric statistics were checked as above, and data were transformed by log (x+1) to meet assumptions.

Results

Physical conditions

During each experiment, oxygen in low-oxygen aquaria fell to target concentrations (1 mg O_2 / L in 1997; 0.5 mg O_2 / L in 1998-1999) during the first 6-10 hours, while high-oxygen tanks remained above 4.5 mg O_2 / L (Fig. 2). Oxygen fluctuated, but average concentrations in low-oxygen tanks remained within 0.2 mg O_2 / L of target oxygen concentrations during 75% of measurements (Fig. 2). In each experiment, oxygen remained near target levels until the fifth day (Fig. 2). Temperatures ranged from 20.1 to 26.7 ^{o}C, similar to the temperature range encountered by York River epifaunal animals in summer (Sagasti et al. in press). At the end of experiments, pH ranged from 7.5-8.2, suggesting that hypercapnia did not occur.

Mortality

Hypoxia tolerance varied greatly among species, with percent mortality in low oxygen ranging from 0 to 100% (Table 2). Some species (2 of 7 at 1 mg O_2 / L and 6 of 14 at 0.5 mg O_2 / L) had LT_{50}s of less than 5 days, a typical duration for hypoxia in the York River, while others (3 of 7 at 1 mg O_2 / L and 5 of 14 at 0.5 mg O_2 / L) were so

tolerant of low oxygen conditions (0.5 -1 mg O_2 / L) that they had no mortality during our experiments (Table 2). At 1 mg O_2 / L (1997), the flatworm *Stylochus ellipticus*, the nudibranch *Doridella obscura* and the mud crab *Neopanope sayi* were among the least tolerant species, while the snail *Mitrella lunata*, the anemone *Diadumene leucolena* and the serpulid polychaete *Hydroides dianthus* were highly tolerant (Table 2). At 0.5 mg O_2 / L (1998-1999), *N. sayi*, the polychaetes *Polydora cornuta* and *Nereis succinea* and the blue crab *Callinectes sapidus* had low survival, while all *D. leucolena*, *H. dianthus*, the hydroid *Obelia bicuspidata* and the polychaete *Sabellaria vulgaris* survived (Table 2). Percent mortality in high oxygen varied between 0 and 14%, and in 19 out of 25 species trials there was no mortality in high oxygen (Table 2).

Survival time decreased as oxygen fell for species tested at both target low-oxygen concentrations. For example, LT_{50} for the nudibranch *Doridella obscura* dropped from 4.65 days at 1 mg O_2 / L to 2.98 days at 0.5 mg O_2 / L; this difference was significant because 95% confidence intervals did not overlap. LT_{50} for the mud crab *Neopanope sayi* dropped from greater than 5 days at 1 mg O_2 / L to 1.31 days at 0.5 mg O_2 / L (Table 2). Although we did not observe sufficient mortality to predict confidence intervals for *N. sayi* at 1 mg O_2 / L, the trend is consistent with decreased survival as oxygen falls. One species, the snail *Mitrella lunata* went from highly tolerant (no mortality) at 1 mg O_2 / L to an LT_{50} of greater than 5 days at 0.5 mg O_2 / L (Table 2). Although the confidence interval for M. lunata at 0.5 mg O_2 / L is large, the data are again consistent with a trend of decreased survival in lower oxygen. The anemone *Diadumene leucolena* and the serpulid polychaete *Hydroides dianthus* were highly tolerant of both target concentrations; with no mortality at either low oxygen level.

The order of species from least to most tolerant was similar but not identical at both target low oxygen concentrations. At both concentrations, the anemone *Diadumene leucolena* and the polychaete *Hydroides dianthus* were among the most tolerant, while the nudibranch *Doridella obscura* and the mud crab *Neopanope sayi* were among the least

tolerant (Table 2). However, *N. sayi* was more tolerant than *D. obscura* at 1 mg O_2 / l, but less tolerant at 0.5 mg O_2 / L (Table 2).

We tested some species twice at a single target low oxygen concentration to determine if LT_{50}s remained consistent, and found that although there was some variation between experiments for single species, but this did not change overall patterns. For 3 out of 4 species (the mud crab *Neopanope sayi*, the snail *Mitrella lunata*, and the bryozoan *Membranipora tenuis*), tolerance relative to other species did not change (Table 2). LT_{50}s during two separate experiments for the polychaete *Nereis succinea* at 0.5 mg O_2 / L differed by 0.93 days, enough to change the order of its tolerance relative to the nudibranch *Doridella obscura* and the polychaete *Polydora cornuta*, but 95% confidence intervals of the two *N. succinea* trials overlapped (Table 2).

Sub-lethal behavioral responses

Many species responded to low oxygen with distinctive behaviors that we did not observe in high oxygen. These behaviors remained consistent when a single species was tested in multiple years and in different oxygen concentrations. For example, in all experiments mobile species in low oxygen (crabs *Neopanope sayi* and *Callinectes sapidus*, flatworm *Stylochus ellipticus*, snail *Mitrella lunata*, nudibranchs *Doridella obscura* and *Cratena kaoruae*, and polychaete *Nereis succinea*) climbed to the tops of their cages, but in high oxygen we were just as likely to find them on the bottom or sides of cages. In addition, although C. kaoruae laid eggs throughout the experiment in high oxygen, it stopped laying eggs after one day in low oxygen. *N. succinea* remained on the cage side at all times in high oxygen, but in low oxygen they floated freely after three days. The tube worms *Hydroides dianthus*, *Polydora cornuta* and *Sabellaria vulgaris* each partially left their tubes and extended their bodies into the water column. In low oxygen, the barnacle *Balanus improvisus* extended feeding appendages into the water column, but did not move them back and forth as if feeding, as they did in high oxygen. *Molgula manhattensis*

elongated its body and siphons, so that siphons were higher above the substrate in low oxygen conditions. The anemone *Diadumene leucolena* elongated its body and extended tentacles higher in the water column; subsequently it released its pedal disc from the substrate and floated, reattaching after oxygen concentrations increased. The bryozoans *Membranipora tenuis* and *Conopeum tenuissimum* responded to hypoxia by forming brown bodies, a resting state that could help them decrease metabolism and wait until oxygen rose before resuming normal activities (Brusca and Brusca 1990). Unfortunately, we did not record proportions of bryozoan zooids that formed brown bodies, but this response occurred to some extent in all colonies in low oxygen, and was rare or absent from bryozoans in high oxygen. Although we observed clear rings of new zooids around all high oxygen *M. tenuis* colonies by the fourth day, we did not observe any growth of new zooids for *M. tenuis* in low oxygen.

Feeding and predation

Colonies of the hydroid *Obelia bicuspidata* started out with similar numbers of hydranths per stem in both oxygen treatments (Fig 3). During the experiment the number of hydranths increased in high but not in low oxygen (Fig 3). Repeated measures ANOVA shows a significant time * oxygen interaction (Table 3), because the difference between high and low oxygen increased with time (Fig 3). At the end of the experiment, hydroids had grown more in high oxygen and had more hydranths with which to feed. The two treatments also differed in the percentage of hydranths that fed, with repeated measures ANOVA showing significantly higher percentages of hydranths feeding in high oxygen vs. low oxygen (Table 3).

The effect of oxygen on predation depended on the predator species and the timing of predation (Figs. 4-7). With two separate prey items (the polychaete *Nereis succinea* and the barnacle *Balanus improvisus*), the mud crab *Neopanope sayi* showed decreased predation towards the end of experiments, but not at the beginning (Fig. 4, Table 4). Low

oxygen significantly decreased predation by flatworms *Stylochus ellipticus* on the barnacle *Balanus improvisus* (23-28 June 1997) (Fig. 5, Table 4). The nudibranch *Doridella obscura* showed significantly decreased predation on the bryozoan *Membranipora tenuis* in low oxygen (Fig. 6, Table 4). In contrast, blue crab juveniles (*Callinectes sapidus*) did not significantly change feeding rates on barnacles *Balanus improvisus* (19-25 July 1998) (Fig. 7, Table 4). However, because so many blue crabs died during the experiment, more barnacles survived in hypoxia (52 of 60 barnacles in all replicates combined) than in normoxia (34 of 60 barnacles in all replicates combined).

Predation during vs. following hypoxia

We observed no mortality of mud crabs (*Neopanope sayi*) during this experiment, and less than 5% of barnacles (*Balanus improvisus*) died from exposure to hypoxia. Mud crabs in high oxygen consumed an average of 10 barnacles during the first two days and 12 barnacles by the end of the experiment (Fig. 7). In low oxygen, crabs ate only an average of 1 barnacle during the first 2 days; after oxygen levels were raised, though, they increased feeding rates so that they had consumed approximately 9 barnacles by the end of the experiment (Fig. 7). ANOVA showed a significant time * oxygen interaction, presumably because during the first 2 days crabs ate more barnacles per day in high oxygen than in low oxygen treatments, but during the last 3 days of the experiment, when oxygen was high in both treatments, crabs compensated for their energetic deficit by eating more barnacles per day in low oxygen treatments (Table 4).

Discussion

Epifaunal species in the York River estuary have relatively high tolerance for hypoxia, that explains in part how they persist in areas periodically exposed to low oxygen (Sagasti et al. in press). Many species had LT_{50}s greater than 7 days (3 of 6 species at 1

mg O_2 / L and 6 of 14 species at 0.5 mg O_2 / L) (Table 2), the maximum duration for typical hypoxic episodes in the York River (Kuo and Neilson 1987). These species probably experience little or no mortality from low oxygen during typical hypoxic episodes in the York River. Species with shorter LT_{50}s could experience considerable mortality during hypoxic episodes, and yet they are still abundant in areas where hypoxia occurs (Sagasti et al. in press). These species may survive in hypoxic areas for three reasons. First, oxygen in the York River fluctuates not only with the neap / spring tidal cycle, but also with daily flood and ebb tides (Kuo and Nielson 1987). Therefore, epifaunal animals in hypoxic areas of the York River experience hourly oxygen variation, and the lowest oxygen concentrations (near anoxia) generally last for only a few hours. Animals could experience frequent brief (hours) periods of normoxic (> 2 mg O_2 / L) or mildly hypoxic (1.5 - 2 mg O_2 / L) oxygen concentrations in the middle of severe hypoxic episodes (Diaz et al. 1992, Pihl et al. 1992), allowing them to recover. Future experiments should test long term survival when hypoxic conditions are interrupted frequently by high oxygen spikes. Second, many species can re-colonize quickly after oxygen rises, or even recruit during hypoxia, allowing populations to re-establish themselves rapidly following hypoxic episodes (Sagasti et al. in prep.). Third, epifaunal species in the Chesapeake Bay grow quickly (Abbe 1987), which may allow animals to grow considerably between hypoxic episodes.

The tolerance of oxygen stress by a given species varies with many factors including temperature, salinity (Herreid 1980), sex (Gerhardt and Baden 1998), age (Eriksson and Baden 1997), season (Legeay and Massabuau 2000), exposure to contaminants (de Zwaan and Eertman 1996) and reproductive status (Vopel et al. 1998), so if we repeated this study under different conditions LT_{50} for some species might change. Consequently, the results of this study serve as a guide for comparing the relative tolerance of different species in this community to low oxygen but do not necessarily apply to all circumstances or habitats. For example, we did not expose animals to increased sulfide that may accompany hypoxia in the

environment and which could have changed survival (Theede et al. 1969). However, hypoxia tolerance mirrors H_2S tolerance for many species, and high sulfide concentrations in the water column are only common in chronically anoxic environments (Theede et al. 1969). Epifauna in the York River rarely experience anoxia and so are relatively unlikely to encounter high H_2S. We believe our results reasonably approximate the relative hypoxia tolerance of epifaunal species in the York River for two reasons. First, we found consistent LT_{50}s when we tested a single species in multiple experiments, even though temperature, salinity, and the presence of other species differed among experiments. Second, the order of species when rated from least to most tolerant remained similar at different oxygen concentrations.

Hypoxia tolerance shows broad patterns among taxonomic groups, with polychaetes, mollusks, platyhelminths and cnidarians being relatively tolerant while crustaceans and vertebrates are relatively intolerant (Mangum and van Winkle 1973; Diaz and Rosenberg 1995). Nevertheless, tolerance of hypoxia can vary as much among species in a single taxonomic group as among species in different groups (McMahon and Russell-Hunter 1978). In this study, we found high variability in tolerance among related species. For example, at 0.5 mg O_2 / L, polychaete LT_{50}s varied from 2.57 days (*Polydora cornuta*) to highly tolerant with no mortality (*Sabellaria vulgaris* and *Hydroides dianthus*), and among crustaceans, LT_{50}s at 0.5 mg O_2 / L varied from 1.31 days (*Neopanope sayi*) to 6.41 days (*Balanus improvisus*) (Table 2). For some taxonomic groups such as hydroids and bryozoans, this study is among the first to measure hypoxia tolerance. We found high tolerance of low oxygen for both hydroids and bryozoans (Table 2).

We found trends of decreased tolerance among mobile species relative to sessile species. For example, at 1 mg O_2 / L, mobile species accounted for the 5 least tolerant species out of 7 species tested, and at 0.5 mg O_2 / L mobile species accounted for 5 of the 7 least tolerant species out of 14 species tested. These trends are consistent with the findings of others in intertidal epifaunal communities exposed to wave stress, where mobile species

were also the least tolerant (Menge 1978, Menge and Sutherland 1987), suggesting that mobile species may have decreased tolerance for physiological stresses as they do for physical stresses. These results also support consumer stress models (Menge and Sutherland 1987, Menge and Olson 1990), which suggest that mobile predators have lower tolerance of stress than sessile prey, leading to a decrease in the importance of predation in stressed communities.

Although many species showed little or no mortality in low oxygen, hypoxia changed behavior in all species, suggesting that hypoxia's greatest effects on epifauna in the York River may be through sub-lethal behavioral changes. As others have found for infauna, species responded to low oxygen with behaviors that allowed them to reach higher oxygen concentrations, escape hypoxic areas, or decrease metabolism (Hagerman 1998). For example, all mobile animals in low oxygen clung to the tops of their cages. Presumably in nature these animals would climb shells, rocks or other structures to reach higher into the benthic-boundary layer where oxygen concentrations increase logarithmically with height above the bottom (Jørgensen 1980, Diaz and Rosenberg 1995). Many sessile species also reached higher into the water column. Presumably, reaching higher oxygen concentrations in the water column could allow animals to transport oxygen back to tissues attached to the bottom. Animals that stretch out into the benthic boundary layer also benefit from increased exposure to flow which reduces their diffusive boundary layer thickness, thus increasing the flux of oxygen to their bodies. The anemone (*Diadumene leucolena*) elongated its body and extended it higher into the water column, then eventually released its pedal disk and floated. Sassaman and Mangum (1972) hypothesized that anemones elongate in hypoxia to increase their surface area to volume ratio, thus increasing the flux of oxygen to tissues. Sassaman and Mangum (1972) did not observe anemones releasing their pedal discs; possibly this behavior does not occur in the species they investigated. In our experiments *Diadumene leucolena* reattached to hard substrates after oxygen increased, thus, floating away from hypoxic areas may represent an escape behavior. The polychaete *Nereis*

succinea also floated into the water column after prolonged hypoxia, and may escape hypoxic areas by floating away. Other species responded to low oxygen with behaviors that may decrease metabolism, such as entering resting states (bryozoans) and decreasing reproductive activities (nudibranch *Cratena kaoruae*).

Although these sub-lethal effects stopped after oxygen increased, in our experiments they disrupted normal behaviors for several days. Most Chesapeake Bay epifaunal species live only one season (Abbe 1987), so short disruptions in an animal's normal behaviors could disrupt a considerable portion of that animal's lifetime and make it less likely that they could reproduce. In the York River, hypoxic episodes occur several times during each growing season, and benthic animals are thus likely to experience sub-lethal hypoxic effects throughout their lifetimes.

A further sub-lethal effect of hypoxia in some epifaunal species may be decreased feeding and growth, which could lead to changes in competitive abilities. For example, growth of new zooids occurred on the edges of colonies of the bryozoan *Membranipora tenuis* in high but not low oxygen. The hydroid *Obelia bicuspidata* was among the most tolerant species in this system, with no mortality during our experiments, yet *O. bicuspidata* showed substantially decreased growth in low oxygen (Fig 3, Table 3). *O. bicuspidata* hydranths were also significantly less likely to feed in low oxygen, which presumably contributed to the decreased growth. Many sessile epifaunal species compete with other species for space and capture space by lateral growth of colonies (Jackson 1979). Therefore, decreased growth during hypoxia may reduce the ability of some species to capture space and compete. However, epifaunal species in the Chesapeake Bay have high growth rates (Abbe 1987) and may be able to compensate for slow growth during hypoxia by growing rapidly between hypoxic episodes. In other words, hypoxic stress may be too infrequent relative to growth rates of the common species to affect community structure appreciably (Huston 1979).

It is likely that hypoxia decreases predation by small epifaunal predators on other epifaunal species for two reasons. First, low oxygen decreased predation rates of mud crabs *Neopanope sayi*, flatworms *Stylochus ellipticus* and nudibranchs *Doridella obscura*. These species are among the most abundant predators in this community (Sagasti et al. in press) and have major effects on population abundance and community structure in Chesapeake Bay epifaunal communities (Branscomb 1976, Marsh 1976, Rheinhardt and Mann 1990). Second, predators were among the species least tolerant of hypoxia, so it is possible that many of them die during hypoxic episodes. Thus, even though juvenile blue crabs (*Callinectes sapidus*) did not decrease feeding rates on barnacles, so many crabs died in hypoxia that fewer barnacles were eaten.

Decreased predation during hypoxia could lead to species using hypoxic episodes as predation refuges. This may be especially true because many prey species were more tolerant of hypoxia than their predators and would experience lower direct mortality from hypoxia. However, when we compared predation during vs. following hypoxia for a highly tolerant prey (barnacles *Balanus improvisus*) and an intolerant predator (mud crabs *Neopanope sayi*), we found that, although crabs had decreased feeding during hypoxia, they increased feeding following hypoxia. Therefore, prey in areas with hypoxic episodes may only have temporary reprieves from predation during hypoxic episodes, after which predation catches up to that in high-oxygen areas. It is likely that the use of hypoxic areas as predation refuges depends on the relative tolerance of predators and prey, and on the duration of hypoxia. During short hypoxic episodes, predators may temporarily decrease feeding but then increase feeding after oxygen increases, leading to no net benefit for the prey. During longer hypoxic episodes, predators could have decreased feeding and high mortality, leading to reduced mortality for prey (but this refuge may be compromised by lower prey growth during hypoxia). Finally, prolonged hypoxia may lead to death of both predators and prey.

Unlike other systems where hypoxia tolerance has major effects on species distributions (Prasada Rao and Ganapati 1968, McMahon and Russel-Hunter 1978, Marshall and McQuaid 1993, Nielsen and Hagerman 1998), the distribution of epifaunal species in the York River did not correlate with hypoxia tolerance (Sagasti et al. in press), suggesting that hypoxia is not a major factor determining distributions in this system. If hypoxia tolerance controlled distributions, we would expect to find increased abundance of the most tolerant species and decreased abundance of intolerant species in areas with the lowest oxygen. However, in a companion study (Sagasti et al. in press) we found that basins in the York River where hypoxia is most severe have greatly increased abundances of the polychaete *Polydora cornuta*, a species that in this study was among the most susceptible to hypoxia. Possibly distributions of *Polydora cornuta* are greatly affected by recruitment density, which for this species is increased in the downstream area (Sagasti et al. in prep.). Areas with lowest oxygen also had decreased abundances of the polychaete *Sabellaria vulgaris* and the bryozoans *Membranipora tenuis* and *Conopeum tenuissimum*, species that were highly tolerant of hypoxia in this study.

The York River epifaunal community appears to be highly resistant to low oxygen stress for several reasons. First, many species can survive hypoxia for over a week, and the York River experiences relatively short hypoxic episodes (up to 7 days). Second, species have behavioral mechanisms that allow them to increase oxygen flux to their bodies, such as reaching higher into the water column. Third, species with high mortality during low oxygen may maintain populations with high recruitment, which can occur even during hypoxic events (Sagasti et al. in prep.). Finally, although many species reduce feeding and predation during hypoxia, leading to reduced growth, high food availability in the Chesapeake Bay (Kemp et al. 1997) may allow species to grow quickly between hypoxic episodes. In summary, the species in this community can not only withstand hypoxic stress but also recover quickly between hypoxic episodes. These characteristics may become even

more important as increased eutrophication increases hypoxic stress in this system (Diaz and Rosenberg 1995).

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Table 1. Experimental details showing for each experiment the species tested (number of individuals per replicate or area covered by species), their diet, and mortality criteria.

Species	Diet	Mortality Criterion
7 - 12 June 1997		
Neopanope sayi (1)	worm (*Nereis succinea*)	no response after several hours of high oxygen
23 - 28 June 1997		
Neopanope sayi (1)	barnacle (*Balanus improvisus*)	no response after several hours of high oxygen
Stylochus ellipticus (2)	barnacle (*Balanus improvisus*)	releases substrate; disintegrates
Mitrella lunata (1)	none	no response after several hours of high oxygen
19 - 24 August 1997		
Diadumene leucolena (5)	filter feeding block	no response after several hours of high oxygen
Hydroides dianthus (1)	filter feeding block	no response after several hours of high oxygen
24 - 29 August 1997		
Mitrella lunata (2)	none	no response after several hours of high oxygen
Doridella obscura (1)	bryozoan (*Membranipora tenuis*)	releases substrate; disintegrates
Cratena kaoruae (2)	hydroid (*Obelia bicuspidata*)	releases substrate; disintegrates
7 - 11 June 1998		
Molgula manhattensis (1)	algae paste, filter feeding block	no response after several hours of high oxygen
Membranipora tenuis (1)	algae paste, filter feeding block	zooid turns black
Polydora cornuta (1 cm^2)	algae paste, filter feeding block	out of tube; disintegrates

19 - 25 July 1998		
Callinectes sapidus (1)	barnacle (*Balanus improvisus*)	no response after several hours of high oxygen
Mitrella lunata (4)	none	no response after several hours of high oxygen
Doridella obscura (3)	bryozoan (*Membranipora tenuis*)	releases substrate; disintegrates
11 - 16 August 1998		
Hydroides dianthus (1)	algae paste, filter feeding block	no response after several hours of high oxygen
Diadumene leucolena (1)	algae paste, filter feeding block	no response after several hours of high oxygen
21 - 26 June 1999		
Balanus improvisus (1)	algae paste, liquid filter feeder food	turns black, disintegrates
Conopeum tenuissimum (1)	algae paste, liquid filter feeder food	zooid turns black
Membranipora tenuis (1)	algae paste, liquid filter feeder food	zooid turns black
Nereis succinea (1)	none	no response after several hours of high oxygen
15 - 20 August 1999		
Sabellaria vulgaris (1)	algae paste, liquid filter feeder food	no response after several hours of high oxygen
Nereis succinea (1)	none	no response after several hours of high oxygen
Neopanope sayi (1)	barnacle (*Balanus improvisus*)	no response after several hours of high oxygen
Obelia bicuspidata (1 cm^2)	*Artemia* sp., live plankton	no growth after days in high oxygen

Table 2. Median Lethal Time (LT_{50}) of epifaunal species in low oxygen treatments in 1997 (target oxygen concentration 1 mg O_2 / L) and 1998-1999 (target oxygen concentration 0.5 mg O_2 / L), and cumulative percent mortality of epifaunal species in low and high oxygen treatments. Some species were tested twice at a single target oxygen concentration; for these species we also include the date of each experiment. For species with LT_{50} greater than 5 days (the duration of the experiments), confidence intervals are large or the model was not able to compute them, so they are not listed. Species with no mortality during experiments are simply labeled tolerant to 5 days.

Species	LT_{50} (days) (95% CI)	Percent Mortality	
		Low-oxygen	High-oxygen
1997 (target oxygen concentration 1 mg O_2 / L)			
Stylochus ellipticus	3.12 (2.13 - 5.44)	59	14
Doridella obscura	4.65 (3.41 - 58.06)	50	0
Neopanope sayi, 7-12 June, 1997	> 5	40	0
Neopanope sayi, 23-28 June, 1997	> 5	37	0
Cratena kaoruae	> 5	14	0
Mitrella lunata, 23-28 June, 1997	tolerant to 5 days	0	0
Mitrella lunata, 24-29 August, 1997	tolerant to 5 days	0	0
Diadumene leucolena	tolerant to 5 days	0	0
Hydroides dianthus	tolerant to 5 days	0	0

1998-1999 (target oxygen concentration 0.5 mg O_2 / L)			
Neopanope sayi	1.31 (0.40 - 1.92)	90	0
Callinectes sapidus	2.56 (1.91 - 3.18)	90	0
Nereis succinea, 21-26 June, 1999	2.57 (1.89 - 3.21)	80	0
Nereis succinea, 15-20 August, 1999	3.50 (2.75 - 4.67)	70	0
Polydora cornuta	2.89 (1.39 - 4.59)	90	4
Doridella obscura	2.98 (2.68 - 3.27)	100	3
Molgula manhattensis	4.49 (3.98 - 5.35)	70	0
Mitrella lunata	> 5	45	0
Balanus improvisus	> 5	20	0
Membranipora tenuis, 7-11 June, 1998	> 5	28	8
Membranipora tenuis, 21-26 June, 1999	tolerant to 5 days	0.5	0.1
Conopeum tenuissimum	tolerant to 5 days	0	0.5
Diadumene leucolena	tolerant to 5 days	0	0
Hydroides dianthus	tolerant to 5 days	0	0
Obelia bicuspidata	tolerant to 5 days	0	0
Sabellaria vulgaris	tolerant to 5 days	0	0

Table 3. Repeated measures ANOVA for the effect of oxygen treatment (high vs. low) and time on a) the number of hydranths per stem and b) the percentage of hydranths that ate, on each sampling date, for colonies of the hydroid *Obelia bicuspidata*.

a.

Source	DF	SS	MS	F	P
Within Subjects					
Time	4	0.918	0.229	5.43	0.0007
Time* Oxygen	4	1.147	0.287	6.78	0.0001
Error	72	3.044	0.042		
Between Subjects					
oxygen	1	4.104	4.101	8.64	0.0088
Error	18	8.549	0.475		

b.

Source	DF	SS	MS	F	P
Within Subjects					
Time	4	5201.742	1300.436	2.35	0.0622
Time* Oxygen	4	4361.967	1090.491	1.97	0.1081
Error	72	39835.421	553.269		
Between Subjects					
oxygen	1	21138.252	21138.252	28.42	0.0001
Error	18	13387.048	743.725		

Table 4. Results of repeated measures ANOVA for the effect of oxygen treatment (high vs. low) and time (during hypoxia vs. following hypoxia) on the number of barnacles eaten by mud crabs (*Neopanope sayi*) per day.

Source	DF	SS	MS	F	P
Within Subjects					
Time	1	0.173	0.173	3.00	0.1003
Time* Oxygen	1	2.149	2.149	37.30	0.0001
Error	18	1.037	0.058		
Between Subjects					
oxygen	1	0.081	0.081	2.04	0.1705
Error	18	0.715	0.040		

Fig. 1. a. View of experimental aquaria from the side. Small and large cages housed mobile epifauna. b. View of experimental aquaria from above.

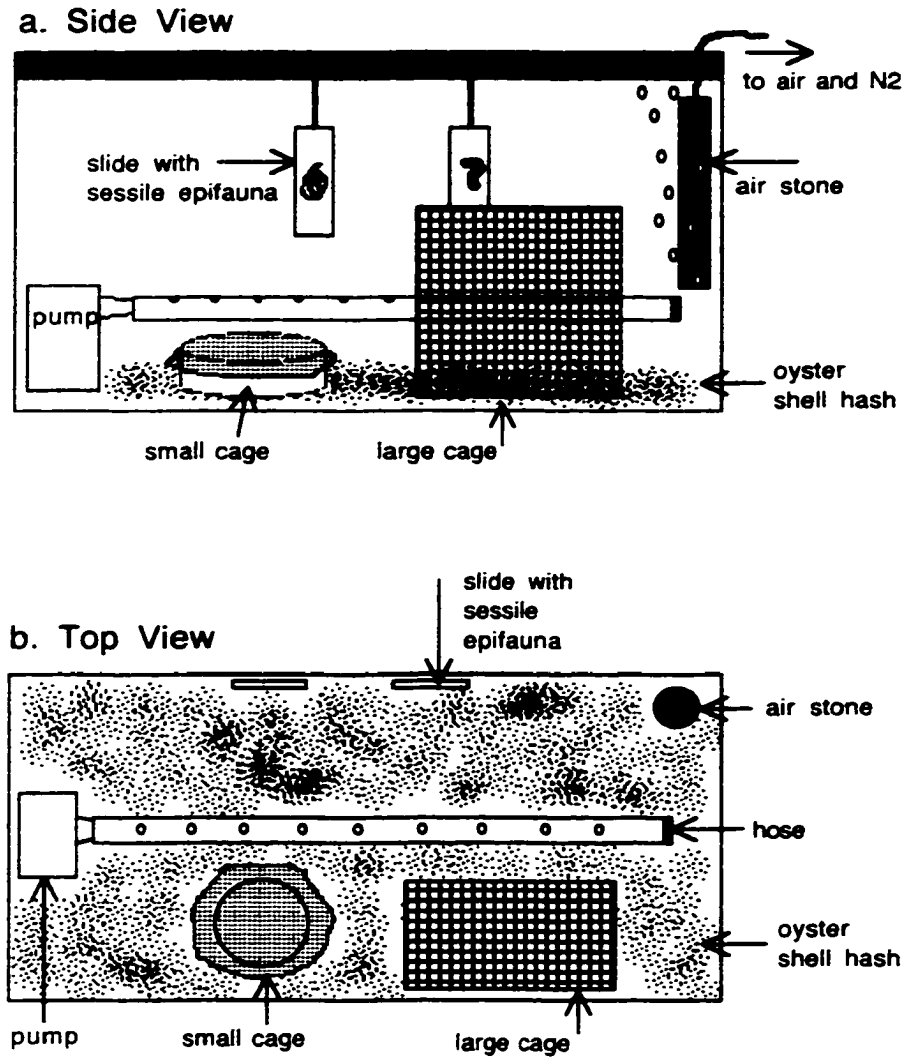


Fig. 2. Oxygen concentrations (mean ± 1 standard error) in aquaria during experiments. Reference lines mark target oxygen concentrations in low-oxygen treatments (0.5 or 1.0 mg O_2 / L). Some error bars are difficult to see because standard errors were small.

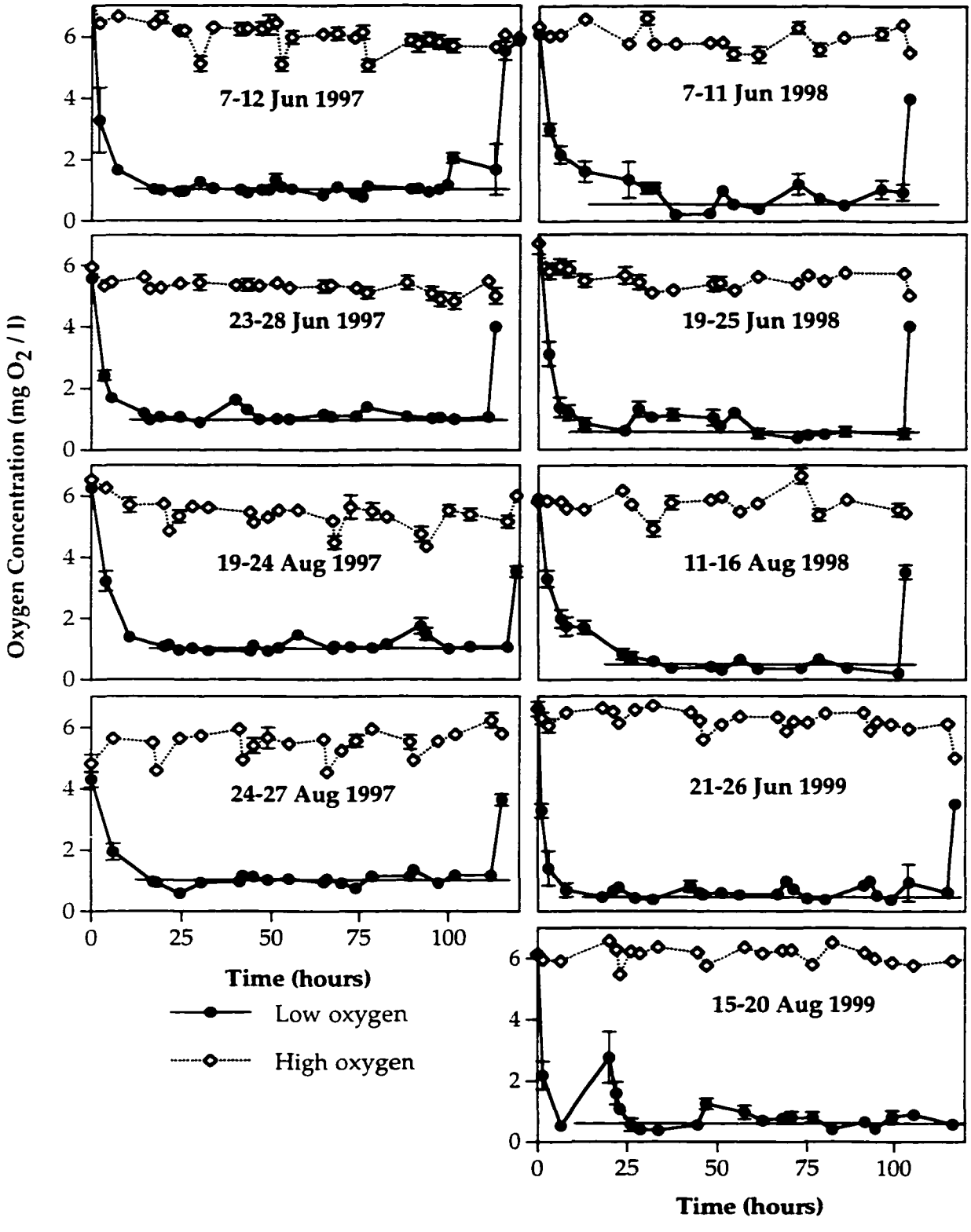


Fig. 3. a. Number of *Obelia bicuspidata* hydranths / stem (mean ± 1 standard error) and b. percent of hydranths (mean ± 1 standard error) that fed in low- and high-oxygen treatments in 1999.

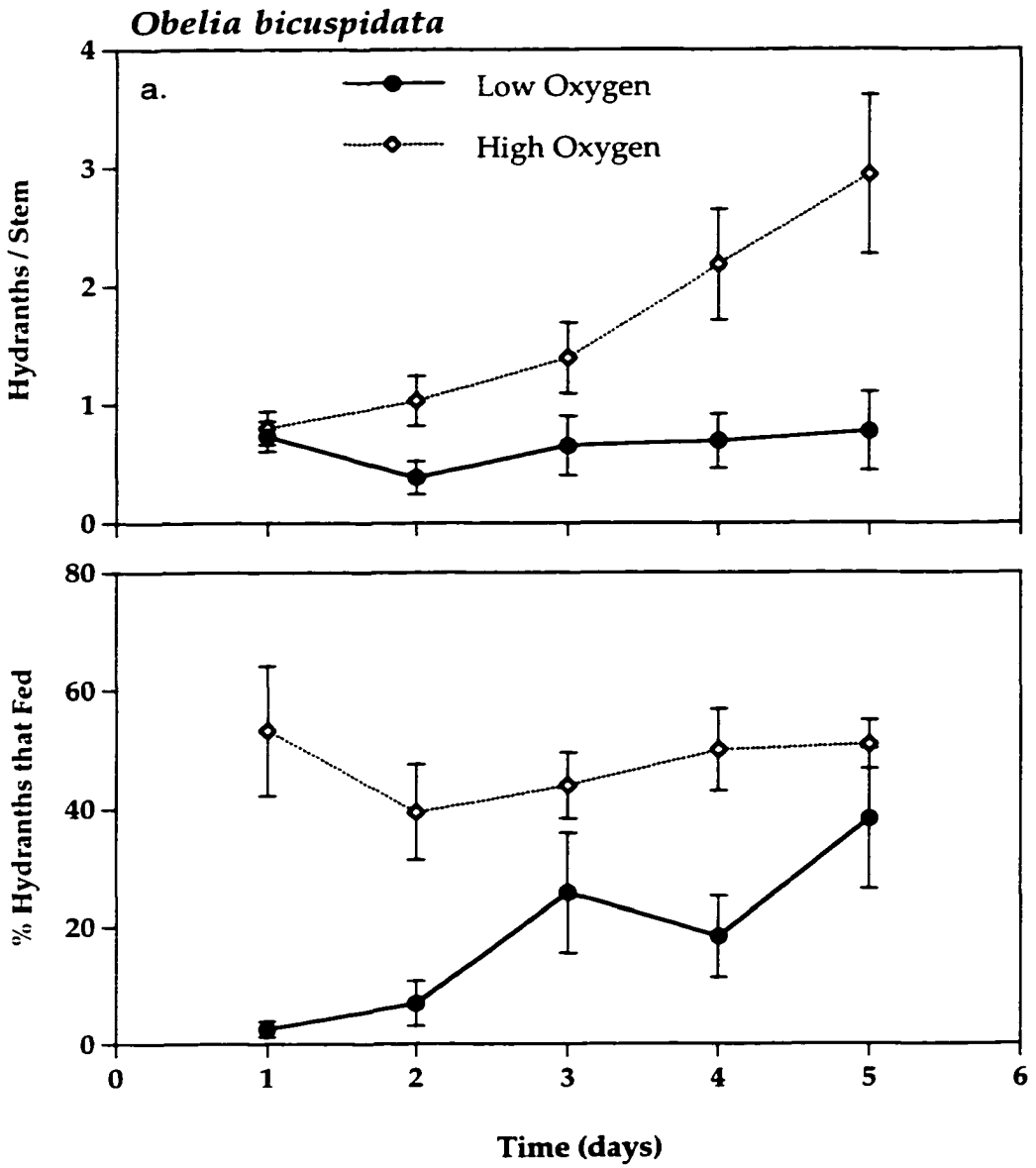


Fig. 4. a. Cumulative number of worms *Nereis succinea* eaten on days 0-1 or 2-4 by the mud crab *Neopanope sayi* in low-oxygen and high oxygen treatments (mean ± 1 standard error) in 1997. b. Cumulative barnacles *Balanus improvisus* eaten on days 0-2 or 3-5 by *N. sayi* in low-oxygen and high oxygen treatments (mean ± 1 standard error) in 1997. Number of replicate crabs (n) are written in bars, and p-values are results of Mann-Whitney tests.

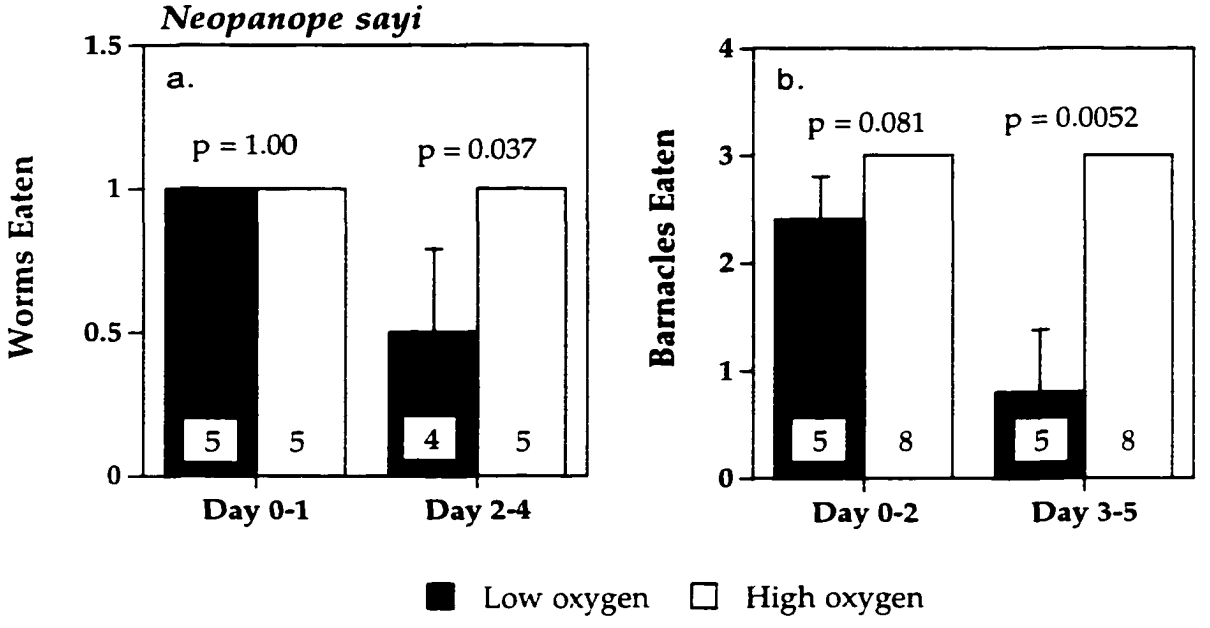


Fig. 5. Cumulative barnacles *Balanus improvisus* eaten by the flatworm *Stylochus ellipticus* in low-oxygen and high oxygen treatments (mean ± 1 standard error) on in 1997. Number of replicate cages with two living flatworms (n) are written in bars, and p-value is the result of a Mann-Whitney U-test.

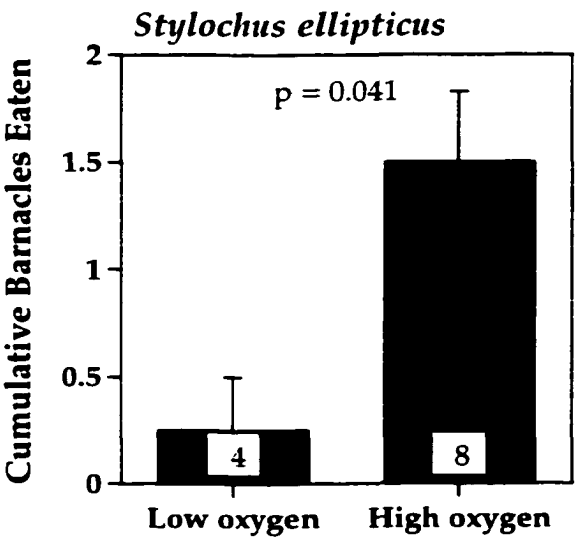


Fig. 6. Effect (percent in predator present minus percent predator absent) (mean ± 1 standard error) of the nudibranch *Doridella obscura* on zooids of the bryozoan *Membranipora tenuis* in low and high oxygen treatments in 1997. Number of replicate nudibranchs (n) are written in bars, and p-value is the result of a Mann-Whitney U-test.

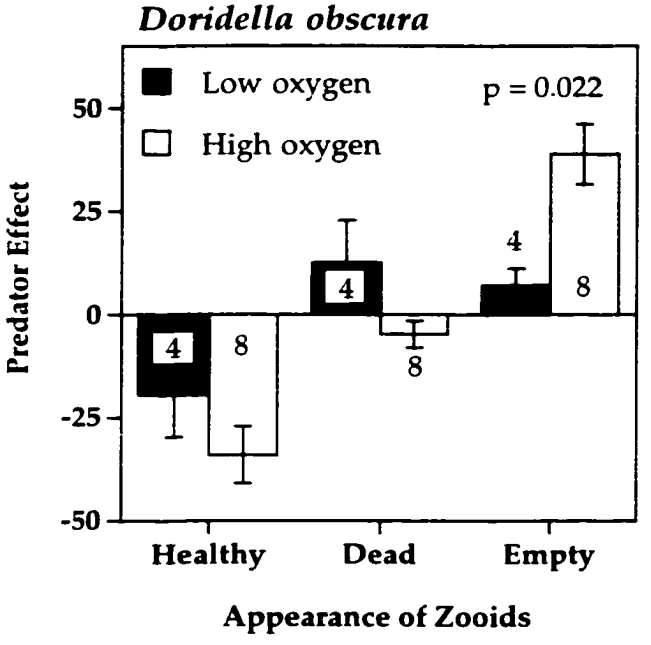


Fig. 7. Cumulative barnacles *Balanus improvisus* eaten daily by juvenile blue crabs (*Callinectes sapidus*) in low-oxygen and high oxygen treatments (mean ± 1 standard error) in 1998. Number of replicate crabs (n) are written in bars, and p-value is the result of a Mann-Whitney U-test comparing barnacles being eaten in days 0-3 in high vs. low oxygen.

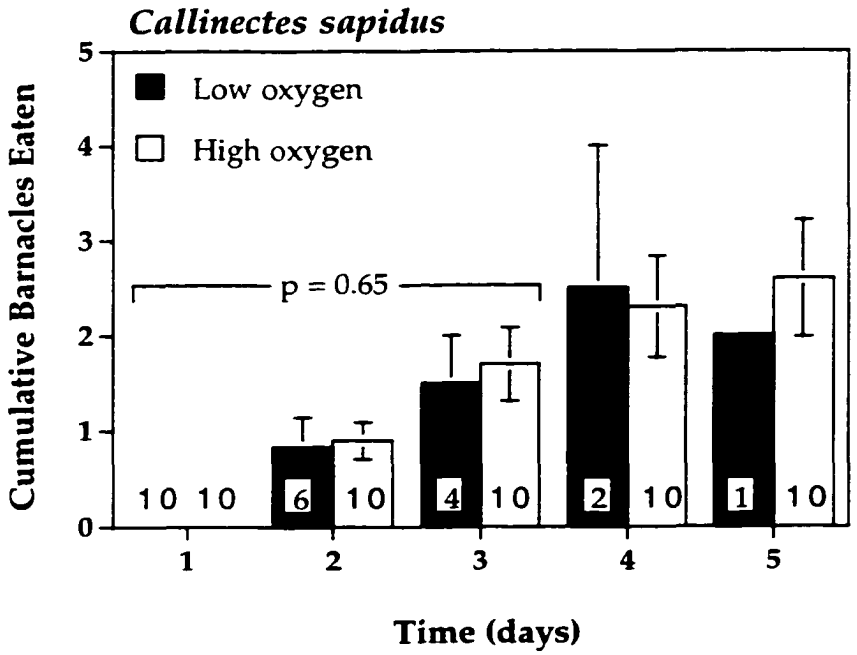
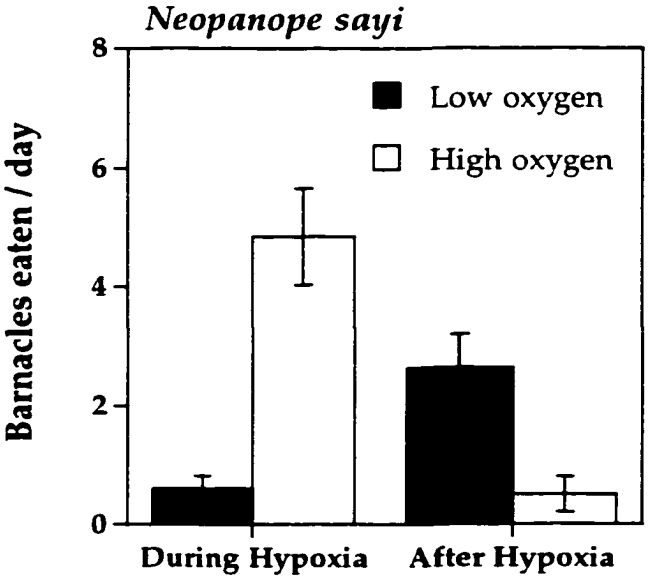


Fig. 8. Cumulative barnacles *Balanus improvisus* eaten daily by the mud crab *Neopanope sayi* in low-oxygen and high oxygen treatments (mean ± 1 standard error) during and following hypoxia. N=10 crabs for all treatments.



Appendix 1. Experimental details showing for each experiment the species tested, their size and number, the substrate on which sessile animals grow or the cages in which mobile animals were kept, diets, and criteria used to determine if animals were dead. We also show sub-lethal behavioral responses which were only observed in hypoxic treatments.

Species	Food	Considered dead when...	Sublethal Responses
7 - 12 June 1997			
Neopanope sayi mud crab 1-2 cm carapace width 1 / large cage	1 worm *Nereis succinea*, 2-3 cm long, on day 0 and another on day 3	no response when touched after several hours normoxia	By day 2, all crabs in hypoxia climbed to top of cages.
23 - 28 June 1997			
Neopanope sayi mud crab 1.1 -2.1 cm carapace width 1 / large cage	barnacles *Balanus improvisus*, 2-3 mm basal diameter, fed 3 on day 1 and 3 again on day 3	no response when touched after several hours normoxia	By day 2, all crabs in hypoxia climbed to top of cages.
Stylochus ellipticus flatworm 2-3 mm length 2 / small cage	5 barnacles, *Balanus improvisus*, 2-3 mm basal diameter	stops holding on to sides of cage; dissintegrates when touched	Many flatworms in hypoxia (but not in normoxia) clung to top of cages throughout experiment.
Mitrella lunata snail 2-3 mm shell length 1 / small cage (barnacles fed with liquid filter feeder food)	none	no response when touched after several hours normoxia	By day 2, all snails in hypoxia climbed to top of cages; extended siphons continuously.

19 - 24 August 1997			
Diadumene leucolena anemone 2 - 4 mm basal diameter 5 / panel	filter feeding block	no response when touched after several hours normoxia	By day 3, all anemones in hypoxia elongated bodies and extended tentacles; by day 5 they released pedal discs and floated free.
Hydroides dianthus serpulid polychaete 1 - 1.5 cm tube length 1 / panel	filter feeding block	no response when touched after several hours normoxia	By day 5, all serpulids in hypoxia extended tentacles and partially left tubes.
24 - 29 August 1997			
Mitrella lunata snail 2 - 3 mm shell length 2 / small cage	none	no response when touched after several hours normoxia	By day 2, all snails in hypoxia (and 10% of snails in normoxia) climbed to top of cages and extended siphons continously.
Doridella obscura nudibranch 2 - 3 mm length 1 / small cage each aquarium also had 1 small cage with bryozoan prey alone	bryozoan *Membranipora tenuis*	stops holding on to sides of cage; dissintegrates when touched	By day 2, all living nudibranchs in hypoxia climbed to top of cages.
Cratena kaoruae nudibranch 2 - 3 mm length 2 / small cage each aquarium also had 1 small cage without *C. kaoruae*, but with its hydroid prey alone	hydroid *Obelia bicuspidata*	stops holding on to sides of cage; dissintegrates when touched	On day 1, nudibranchs in hypoxia and normoxia laid eggs, but only nudibranchs in normoxia laid eggs on days 2-5. By day 2, nudibranchs in hypoxia climbed to top of cages.

(bryozoans and hydroids fed with algae paste and filter feeding blocks)

7 - 11 June 1998			
Molgula manhattensis tunicate 1 - 2 cm diameter 1 / slide	algae paste, filter feeding block	no response after several hours normoxia	By day 3, all living tunicates in hypoxia elongated; extended siphons high into water column.
Membranipora tenuis encrusting bryozoan 1 colony / slide	algae paste, filter feeding block	zooid turns black	Zooids in hypoxia formed brown bodies.
Polydora cornuta polychaete 1 cm^2 section with tubes on slide	algae paste, filter feeding block	out of tube; dissintegrates when touched	By day 3, > 90% of worms in hypoxia partially left tubes; worms in normoxia remained in tubes.
19 - 25 July 1998			
Callinectes sapidus juvenile blue crab 3 - 4 cm carapace width 1 / large cage	6 barnacles, *Balanus improvisus*, 0.75-1.25 cm basal diameter	no response after several hours normoxia	By day 2, all living crabs in hypoxia climbed to top of cages.
Mitrella lunata snail 2 - 3 mm shell length 4 / small cage	none	no response when touched after several hours normoxia	By day 2, all living snails in hypoxia climbed to top of cages and extended siphons continuously.
Doridella obscura nudibranch 2 - 4 mm length 3 / small cage	bryozoan *Membranipora tenuis*	stops holding on to sides of cage; dissintegrates when touched	By day 2, all nudibranchs in hypoxia climbed to top of cages.
(bryozoans and hydroids fed with algae paste and filter feeding blocks)			
11 - 16 August 1998			
Hydroides dianthus serpulid polychaete 1 - 1.5 cm tube length 1 / slide	alage paste, filter feeding block	no response when touched after several hours normoxia	By day 5, serpulids in hypoxia extended tentacles and partially left tubes.

Diadumene leucolena anemone 3 - 5 mm basal diameter 1 / slide	alage paste, filter feeding block	no response when touched after several hours normoxia	By day 2 anemones in hypoxia became elongated and extended tentacles. By day 4, they released pedal discs and floated free.
21 - 26 June 1999			
Balanus improvisus barnacle 3 - 5 mm basal diameter 1 / slide	algae paste, liquid filter feeder food	turns black in shell and dissintegrates when touched	By day 3, all barnacles in hypoxia gaped open with appendages extended.
Conopium tenuissimum encrusting bryozoan 1 colony / slide	algae paste, liquid filter feeder food	zooid turns black	Zooids in hypoxia formed brown bodies or extended lophopores continuously by day 3.
Membranipora tenuis encrusting bryozoan 1 colony / slide	algae paste, liquid filter feeder food	zooid turns black	Zooids in hypoxia formed brown bodies or extended lophopores continuously by day 3. No growth in hypoxic colonies but all normoxic colonies had clear growth rings by day 4.
Nereis succinea polychaete 3 - 4 cm length 1 / small cage	none	no response when touched after several hours normoxia	By day 2, all hypoxic worms climbed to top of cage, by day 4 all had let go and floated free.
15 - 20 August 1999			
Sabellaria vulgaris polychaete 1 - 2 cm tube length 1 / shell	algae paste, liquid filter feeder food	no response when touched after several hours normoxia	All worms extended tentacles and partially left tubes by day 5; never left tubes completely.
Nereis succinea polychaete 2 - 3 cm length 1 / small cage	none	no response when touched after several hours normoxia	By day 2, hypoxic worms climbed to top of cages; by day 4 they let go and floated free.

Neopanope sayi mud crab 1 - 3 cm diameter 1 / small cage with large mesh	8 barnacles *Balanus improvisus*, 2-3 cm basal diameter	no response after several hours normoxia	All hypoxic crabs climbed to top of cages on day 1 and remained there for the rest of the experiment.
Obelia bicuspidata hydroid 1 cm^2 section on slide	*Artemia* sp., live plankton from York River	did not revive after several days normoxia	Number of hydranths reduced compared to normoxic hydroids.

CHAPTER 3: ESTUARINE EPIFAUNA RECRUIT DESPITE PERIODIC HYPOXIC STRESS.

Abstract

The persistence of communities exposed to environmental stress depends in part on recruitment. Recovery from stress-induced disturbance can be slow when stress coincides with the recruitment of dominant species because stress may change the survival or settlement success of propagules. In some estuaries, the recruitment of epifaunal benthic invertebrates coincides with a significant environmental stress, low water column dissolved oxygen, termed hypoxia (≤ 2 mg O_2 / L). To assess the impact of hypoxic stress on recruitment, we measured recruitment of epifaunal taxa in the lower York River, a subestuary of the Chesapeake Bay, USA, that experiences predictable, periodic hypoxia associated with neap/spring tidal cycling during summer. We deployed recruitment substrata in two areas with differing hypoxia levels (upstream and downstream), and allowed epifauna to recruit during periods of low oxygen (neap tides) and high oxygen (spring tides) in 1996 and 1997. Recruitment was consistently high during neap tides, even when severe oxygen depletion (< 0.5 mg O_2 / L) occurred during deployments; indeed, peak recruitment episodes of several dominant epifaunal taxa, and of total epifauna, coincided with hypoxic events during both summers. Recruitment was also consistently high in the downstream study area, even though this area experienced lower oxygen concentrations during hypoxic episodes. We also conducted laboratory experiments exposing larvae of epifauna to high and low oxygen conditions. In these laboratory experiments, there was a consistent pattern of higher recruitment in high oxygen for all taxa, and these differences were significant for

5 of 9 taxa, but recruitment did occur in low oxygen for 7 of 9 taxa. An experiment with the tunicate *Molgula manhattensis* showed that restoration of high oxygen after 1 day of exposure to low oxygen led to recovery and normal recruitment. These results indicate that the larvae of the dominant estuarine epifauna are highly tolerant of oxygen stress. Although hypoxia reduces recruitment in laboratory experiments, it appears to have little effect on recruitment in the field for many epifaunal species in this ecosystem. High larval tolerance of hypoxic stress may allow communities to persist even though the summer hypoxia season coincides with the recruitment of many epifaunal species. Increased recruitment during neap tides suggests that factors besides hypoxia influenced recruitment in the York River; these factors may have included lower current speeds and changes in larval availability. Our results illustrate how the relationship between recruitment and regional-scale stresses, such as hypoxia, may be difficult to predict, since regional-scale stresses are often correlated with numerous other factors.

Introduction

Environmental stress and recruitment are major regulators of community structure and community processes (Menge and Sutherland 1987). Environmental stresses can change the composition, diversity and functioning of communities (Sousa 1984; Peterson and Black 1988; Death and Winterbourn 1995). Similarly, variation in recruitment, the result of settlement, metamorphosis and early survival of propagules (Rodriguez et al. 1993), can influence species distributions, abundances and diversity (Osman and Whitlatch 1998; Hubbell et al. 1999; Smith and Whitman 1999). Stress and recruitment can each change the importance of community processes acting at later life stages, such as competition, predation, disturbance (Menge and Sutherland 1987; Menge 1991), and positive interactions (Bertness and Callaway 1994). Although stress determines the probability and scale of disturbances (Sousa 1984), recruitment, along with dispersal by juveniles and adults, influences the speed of recovery and the composition of the community following disturbance (Palmer et al. 1996; Paine et al. 1998; Whitatch et al. 1998).

Although stress and recruitment both have important effects on communities, the relationship between them is unresolved. Conceptual community models consider the effects of stress and recruitment on species interactions and community structure independently (Connell 1978; Doherty 1981; Menge and Sutherland 1987; Wootton 1998), and do not include interactions between stress and recruitment. If stress has consistent effects on recruitment, the combined effects of stress and recruitment may differ from the separate effects of stress and recruitment. For example, if stress depresses recruitment in a non-linear fashion, high stress and decreased recruitment could act together to decrease the importance of species interactions more than we would predict by adding the effects of stress and recruitment alone.

Stress can alter recruitment at numerous stages, by decreasing fecundity of adults (Sanders 1986; Weimeyer et al. 1988), survival of propagules or settlement patterns

(Connell et al. 1997). For example, stress caused by high currents interfered with the ability of marine invertebrate larvae to reach the substrate and attach (Eckman 1983; Mullineaux and Garland 1993). Conversely, stress can increase settling success by creating disturbances that increase free space available for settlement (Paine 1966, Osman et al. 1989; Minchinton and Scheibling 1993). Finally, stress could alter post-settlement mortality by changing growth or predation rates on recent settlers (Osman et al 1992; Minchinton and Scheibling 1993). Species differ in their tolerance of stress, so the effects of stress may be species-specific (Hurlbut 1991; Mullineaux and Garland 1993) and thus influence community composition. At the community level, the effects of stress on recruitment depend on the timing of stress relative to the recruitment of dominant species (Sousa 1984; Breitburg 1992). Disturbed communities often recover through the arrival of recruits (Sousa 1984) or migration of adults (Palmer et al. 1996). Thus, if the recruitment of dominant species is impeded by stressful events, recovery may be slow, or the community composition may be permanently changed.

Depletion of water-column dissolved oxygen is among the most common environmental stresses affecting coastal systems (Diaz and Rosenberg 1995). Dissolved oxygen concentrations above 2 mg O_2 / L (normoxia) have few deleterious impacts on animals, while oxygen concentrations below 2 mg O_2 / L (hypoxia) often have harmful impacts on animals (Tyson and Pearson 1991). Dissolved oxygen concentrations below 0.1 mg O_2 / L (anoxia) often have severe impacts on ecosystems (Diaz and Rosenberg 1995). Hypoxia and anoxia are becoming more widespread and persistent because of accelerating anthropogenic eutrophication (Officer et al. 1984). Hypoxia can change behavior, decrease growth and kill macrofauna (Forbes and Lopez 1990; Llanso 1991; Diaz and Rosenberg 1995). It can also change the diversity (Llanso 1992), biomass, species composition (Jorgensen 1980; Rosenberg et al. 1983) and function (Schaffner et al. 1992) of benthic communities. Hypoxia can have important effects on community processes such

as predation by altering predator behavior and prey availability (Pihl et al. 1992; Breitburg et al. 1994; Nestlerode and Diaz 1998).

Hypoxia can change recruitment for some species. Exposure to low oxygen caused higher mortality in larvae than in adults of several fish (Saskena and Joseph 1972; Keckies et al. 1996), insect (Nebeker et al. 1996) and bivalve species (Widdows et al. 1989; Wang and Widdows 1991). In contrast, some invertebrate larvae may be highly tolerant of hypoxia. For example, larvae of the clam *Mercenaria mercenaria* showed no change in growth or survival after 24 hours at 1 mg O_2 / L (McMurrer and Miller 1989), and larval survival of the polychaete *Streblospio benedicti* was unaffected by 92 hours at 14.5% saturation (Llanso 1991). Often, larval tolerance increases as larvae develop (Wang and Widdows 1991; Spicer 1995) because the ability to control metabolic expenditures increases with larval stage (Widdows et al. 1989) and because the youngest larvae have reduced defenses such as blood pigments with lower oxygen affinities (Spicer 1995). Larvae of some taxa exposed to hypoxia can stop eating and / or growing (Wang and Widdows 1991; Baker and Mann 1992; Nebeker et al. 1996), leading to delayed development and prolonged larval stages (Widdows et al. 1989; Keckies et al. 1996; Nebeker et al. 1996). Recruitment during hypoxia may be particularly difficult because settlement and metamorphosis require abundant energy, and larvae primarily have energy in the form of fats that cannot be used for anaerobic metabolism (Baker and Mann 1992). Hypoxia decreases settlement of some species; for example oysters (*Crassostrea virginica*) reduced settling rates at oxygen concentrations below 1.5 mg O_2 / l, and completely stopped settling during anoxia (Baker and Mann 1992). The larvae of some species can avoid low oxygen water, resulting in decreased settlement in hypoxic areas (Powers et al. in press).

The implications of hypoxia's effects on recruitment in a particular community will depend in part on the species composition and the timing of hypoxia. If the larvae of dominant species have low hypoxia tolerance, or if some species are more tolerant than others, hypoxia may change the community composition and may indirectly influence

interactions between species. Similarly, if the timing of hypoxia coincides with the recruitment of dominant species, the community composition may shift.

In this study, we used a combination of field monitoring and laboratory recruitment experiments to examine the effects of hypoxia on recruitment in an estuarine epifaunal community. In this system, the timing of hypoxia coincides with the recruitment of dominant species, yet the community persists (Sagasti et al. in press). Our objectives were to determine 1) whether low-oxygen events decrease recruitment by the larvae of epifaunal species in the field and 2) whether low-oxygen changes the recruitment of epifaunal species in the laboratory. By examining the relationship between hypoxic stress and recruitment, we hope to understand how epifaunal species persist in an area where hypoxia may deter recruitment.

Methods

Field measurements of recruitment and environmental variables

Recruitment by epifaunal invertebrates was characterized in the York River, Virginia, a subestuary of the Chesapeake Bay, USA, where the timing and spatial extent of hypoxia are relatively predictable (Haas 1977; Kuo and Nielson 1987). The York River experiences well-described cycles of hypoxia ($\leq$ 2 mg O_2 / L) and normoxia (> 2 mg O_2 / L) in the summer (Haas 1977). During spring tides, tidal currents are sufficient to destratify the water column, re-oxygenating deep layers and preventing hypoxia. During neap tides, currents are too weak to prevent stratification and hypoxia typically occurs below 9 m (Pihl et al. 1992). During these hypoxic episodes, oxygen concentrations are often lowest near the mouth of the York River and increase upstream (Sisson et al. 1991; Kuo et al. 1993). Therefore, hypoxia usually occurs during neap tides in the summer and is often most severe downstream of Gloucester Point (Fig. 1) (Haas 1977; Kuo et al. 1993). An additional factor often associated with hypoxia is hypercapnia, an increase in water column CO_2

concentrations that can lead to decreased pH (Cochran and Burnett 1996). In the York River pH remains above 7.2 except in the deepest areas (≥ 20 m) following prolonged (more than 24 hours) anoxia (Nestlerode, personal communication).

To compare epifaunal recruitment in high vs. low-oxygen conditions, we collected recruits of dominant species on artificial substrata during both spring and neap tides (corresponding with high and low-oxygen periods) and in two areas (upstream and downstream) (Fig. 1). During hypoxic episodes, dissolved oxygen concentrations in the downstream area are generally lower than concentrations in the upstream area by 0.5-1 mg O_2 / L (Sagasti et al. in press). The two areas are similar in nutrient concentrations (Sin 1998), sediment composition (Nichols et al. 1991), and have similar temperature, salinity, and epifaunal communities (Sagasti et al. in press). Within each area, oxygen concentration is similar between stations (Sagasti et al. in press).

In each area (downstream and upstream) we randomly chose 8 station locations (1996) or 10 station locations (1997) along the 15 m depth contour, where hypoxia generally occurs each summer, but where hypercapnia is unlikely. At each station we placed a sampling unit consisting of a weighted H-shaped PVC pipe frame to which we attached settlement substrates, and a rope leading to a surface buoy (Sagasti et al. in press). The PVC frame floated 0.5 m above the sediment surface in 1996, but this distance was increased to 1-1.5 m in 1997 to ensure that frames remained well above the sediment surface. By the end of the summer in 1996, we had lost the sampling units at half of the stations in each area due to collisions with boats or other accidents. In 1997, sampling units at each station were replaced as soon as they lost and we ended the summer with all stations intact.

Epifauna were allowed to settle on 10 X 10 cm PVC panels. Although PVC is not a naturally available substrate, PVC panels in the York River developed communities with species composition (Sagasti et al. in press) similar to natural communities such as those on oyster shells (Rheinhardt and Mann 1990). Slight variations in the settling substratum can

change larval settlement (Todd 1998), and although it is likely that each species in the York River epifaunal community has different settling preferences, we attempted to make panels as suitable as possible for a wide range of species. Panels were lightly sanded and allowed to develop natural microbial films, which enhance settlement (Coe and Allen 1937; Keough and Raimondi 1996). Panels were attached to the frames oriented perpendicular to the substratum, because panels in this orientation collect the greatest diversity of epifaunal species (Sagasti, unpublished data). Panels were placed into randomly chosen locations on each frame.

Panels were deployed at each station and then retrieved after 2 days. This deployment duration was designed to measure recruitment and early post-settlement processes. We placed one panel at each station during deployments in 1996 and 4 panels at each station during deployments in 1997. We had a total of 10 deployments in 1996, 5 during neap and 5 during spring tides, and 8 deployments in 1997, 4 during neap and 4 during spring tides. All deployments occurred between June and September, coinciding with the season of peak epifaunal recruitment in the Chesapeake Bay (Abbe 1987) and with the maximum occurrence of hypoxia (Officer et al. 1984).

To retrieve panels, the entire PVC frame was brought to the surface by hand (1996) or with a mechanical winch (1997). Panels were then removed and placed into 1-liter containers filled with 10 μm filtered York River water, kept in coolers, and held upright without dislodging or damaging recruits. Panels were systematically searched using a dissecting microscope and all recruits were identified to the lowest possible taxonomic level. Colonial protists were not enumerated because it was impossible to distinguish among colonies. For some groups, such as campanularid hydroids, it is not possible to distinguish between species until recruits are older, thus we could not identify all recruits to species. We counted all recruits within one day of retrieval.

To characterize the larval supply, we also placed one cylindrical larval trap (Yund et al. 1991) at each station during each deployment. The trapping efficiency of cylindrical

larval traps varies with the weight and swimming ability of each species, and with current speed (Butman 1986). Therefore, traps can characterize the kinds of larvae available, but are less reliable for estimating their abundance. Traps consisted of PVC tubes 25 cm long with an inside diameter of 5 cm, capped at the bottom. Before deployments, 50 ml 10 % buffered formalin with Rose Bengal stain was placed in each trap, to enhance retention of larvae and decrease the possibility of predation. We filled the remainder of the tube with 10 µm filtered York River water. We attached traps upright to the PVC frames. After each deployment, we removed the traps, sieved the contents through a 125 µm sieve (1996) or a 63 µm sieve (1997), and fixed the contents in 10 % buffered formalin with Rose Bengal stain. Finally, we used a dissecting microscope to identify all larvae at a minimum of 3 stations in each area of the river during each deployment to the lowest taxon possible.

To characterize the physical conditions during each deployment, we used a combination of data from ongoing VIMS studies and data collected from our stations to parameterize the oxygen concentration, salinity and temperature hourly in each area. In 1996, temperature, salinity and dissolved oxygen were measured in the downstream area from a moored buoy east of Gloucester Point (Fig. 1). This buoy used an array of Hydrolab Datasonde Multiprobes to record conditions at multiple depths, including 13 m and 16 m. To estimate conditions at the depth of our panels (14.5 m), we averaged the data from 13 m and 16 m. In addition, we measured temperature, salinity and dissolved oxygen at the upstream area in 1996 and in both areas in 1997 using a Hydrolab Datasonde Multiprobe at one station in each area (Fig. 1). The Hydrolab was suspended approximately 15 cm above the PVC frame with the sensors oriented toward the frame. After retrieving a Hydrolab, we tested it against standards to make sure it was still calibrated. Readings never differed by more than 0.5 ppt for salinity, more than 0.71° C for temperature, or more than 0.32 mg O_2 / L for oxygen concentration. However, we lost data periodically due to battery or sensor failure.

For each year, we analyzed the number of recruits (all species combined) using a Model I (fixed factor) general linear model ANOVA with factors date, location (upstream or downstream) and tidal stage (neap or spring). Because we consider date to be a blocking factor, we did not include date in interaction terms. Assumptions of ANOVA were assessed using Cochran's test for homogeneity of variance (Underwood 1997) and the Shapiro-Wilkes test for normality (Zar 1996). In 1996, data were transformed by log (x+1) in order to meet the assumption of homogeneity of variances (Zar 1996). In 1997, the data did not meet the assumptions of homogeneity of variance even after transformation. However, because the results of ANOVA were highly significant ($p<0.0001$) and because ANOVA is generally robust to violations of the homogeneity of variance assumption (Zar 1996), we believe the results are still useful. Because we found a significant tide * location interaction in 1997, we performed Model I general linear model ANOVAs between spring and neap tides for each location separately, and between upstream and downstream for each tidal stage separately.

We also analyzed the number of recruits of individual taxa as described above, but only considered taxa that either recruited during at least 3 deployments or comprised a large fraction (greater than 10%) of recruits during a single deployment. Because recruitment was highly seasonal for individual taxa, we included in each analysis only those time periods where average recruitment in at least one location during neap or spring tide was equal to at least 10% of maximum recruitment for that taxa. For a few taxa (in 1996 *Sabellaria vulgaris* and *Hydroides dianthus* and in 1997 *Hydroides dianthus*) we could not meet the assumptions of ANOVA using the tests described above, and so we did not analyze results statistically for these taxa.

Laboratory experiments: hypoxia effects on recruitment

In the field, hypoxia is correlated with environmental factors such as neap tides and low current speeds (Haas 1977) that could themselves influence recruitment processes. To

investigate the effects of hypoxia alone, we exposed larvae to high or low-oxygen conditions in the laboratory and allowed them to settle. Because the relative abundance of larvae of epifaunal species in the York River is highly seasonal, we repeated this experiment five times throughout the summer of 1999 (31 June -1 July, 8-9 July, 15-16 July, 29-30 July, 29-30 August).

For each experiment, we obtained larvae of epifaunal species by collecting natural plankton at an outflow pipe in the VIMS sea water system located on the VIMS oyster pier (Fig. 1). Water for the sea water system is pumped directly from the York River. Although this water flowed through a pump, we collected a wide variety of zooplankton and meroplankton such as copepods and polychaete larvae that were actively swimming and appeared undamaged when viewed with a microscope. Although water was pumped from surface waters, similar epifaunal species are found in surface and deep areas of the York River (Sagasti et al. in press). For each experiment we collected plankton for approximately 45 minutes by allowing water to flow through a 63-mm sieve. We removed ctenophores (to prevent them from eating the other plankton) and large pieces of debris. In the laboratory, we placed the plankton in a beaker with York River water, brought it to a volume of 1 L, and kept it well-mixed with a magnetic stirrer. To buffer the pH and prevent hypercapnia (an increased CO2 concentration and subsequent decreased pH) (Cochran and Burnett 1996), we added 1.5 g of oyster shell dust to the plankton solution. We made the oyster shell dust by sieving oyster shell hash on a 125 μm sieve and collecting the dust that passed through. We used 150 ml of this plankton and oyster shell solution in the following experiments, leaving approximately 850 ml unused. We used only a small portion of the plankton to minimize the difference between the first and last aliquots.

Next, we created low-oxygen water by bubbling York River water (which first passed through a 10 μm filter) with N_2 gas until oxygen concentrations fell below 0.5 mg O_2 / L as measured by an oxygen sensor (YSI Model 58, calibrated daily). This low-oxygen water was carefully siphoned into 25 ml glass scintillation vials without creating

bubbles that could raise oxygen concentrations. We allowed microbial films to form on the surfaces of vials prior to experiments, so that larvae would encounter surfaces similar to those on field panels. We filled each vial until it overflowed, added 3 ml of the plankton solution to the bottom of the vial with a Pasteur pipette, covered the top with plastic film, put a lid on the vial and wrapped it with parafilm to prevent oxygen leakage. After filling vials with low-oxygen water and plankton, we raised the oxygen concentration of the remaining low-oxygen water by bubbling with air until oxygen concentrations reached at least 6.0 mg O_2 / l, and repeated the processes above with vials of high-oxygen water. For the experiment on 31 June -1 July, 15 vials for each treatment (low- and high-oxygen) were prepared. For all further experiments (8-9 July, 15-16 July, 29-30 July, 29-30 August), we prepared 25 vials for each treatment.

We randomly chose 5 vials from each treatment (high- and low-oxygen) to estimate the conditions in vials at the beginning of each experiment. The oxygen concentration in each vial was measured using a YSI Model 58 oxygen meter, calibrated daily. For the last 3 experiments (15-16 July, 29-30 July, 29-30 August), vial contents were then fixed in Formalin, sieved on a 63 μm sieve, and all larvae were identified to the lowest possible taxon using a dissecting microscope. Remaining vials were allowed to stand undisturbed in the dark at 25°C for 24 hours to allow larval settlement. The water in each vial came directly from the York River, and thus presumably had similar salinity and initial chemistry as conditions in the field. Finally, vials had a full complement of common plankton with which larvae would interact in the field, including small predators such as flatworms. Therefore, it was possible for larvae to settle and die before we counted them, and so, like the field measurements, this experiment measures recruitment rather than settlement.

After 24 hours, all surfaces of each vial were examined under a dissecting microscope and recruits that had attached and metamorphosed were counted and identified. In the case of the polychaetes *Polydora cornuta* and *Nereis succinea*, recruits formed mud tubes from debris in the water and were counted if animals could be seen moving inside the

tubes. Recruits on the sides and bottoms of the vials were identified by examining them through the glass. Recruits on the upper surface, which was covered with plastic film, were examined by removing the plastic film and scanning its surface. The vast majority of recruits in both treatments (>95%) settled on the bottom surface of vials. For campanularid hydroids, barnacles and anemones, we could not identify recruits to species. Although *Diadumene leucolena* is the only anemone species recorded in deep waters where our field observations occurred, both *Haliplanella luciae* and *Diadumene leucolena* are found in shallow water, and recruits in laboratory experiments probably consisted of a mixture of these species. Similarly, only *Balanus improvisus* lives in deep water where our field observations occurred, while an additional barnacle species, *Balanus eburneus*, lives in shallow water. After counting recruits, we measured the oxygen concentration and pH in each vial using a YSI model 38 oxygen monitor and a Beckman Φ220 pH meter, each calibrated daily.

For each experiment, we analyzed only those species which recruited in at least 2 vials in any treatment. For each species, we performed a Mann-Whitney U-test with oxygen treatment as the factor and number of recruits per vial as the response variable. For a few species, we found recruitment only in high oxygen. To analyze the results for these species statistically, we performed a 1-sample t-test to determine if recruitment in high-oxygen differed from zero. Because each experiment took place at a different point in the summer recruitment season and experiments had different numbers of replicates, we analyzed species-specific recruitment separately in each experiment. However, all experiments that contained a given species tested the same hypothesis, i.e. that hypoxia reduces recruitment of that species. Thus, for each species that recruited during more than one experiment we combined the probability values from the experiments in which it recruited, as suggested by Sokal and Rohlf (1981, pp. 779).

Laboratory experiments: hypoxia effects on Molgula manhattensis settlement

M. manhattensis is one of the most common epifaunal species in the York River (Sagasti et al. in press), and it is useful for studies of settlement because larvae are easily obtained in laboratory cultures and metamorphosis usually takes place within 1 day of fertilization (Costello et al. 1957). We used swimming tadpole stages (approximately 12-16 hours after fertilization) for experiments.

The first *Molgula manhattensis* experiment evaluated effects of high and low-oxygen on the timing of settlement, and took place on 8-9 June, 1999. For this experiment, 15 replicate high- and low-oxygen vials were created as described above for plankton experiments, except that *M. manhattensis* embryos were substituted for plankton. Five replicates from each treatment were randomly chosen at the beginning of the experiment and destructively sampled to determine starting oxygen concentrations. The remaining 10 replicate vials for each treatment were examined for metamorphosed recruits 9 times over 33 hours. Because we did not want to disturb the vials or change oxygen concentrations, only larvae metamorphosed on the bottom and side surfaces of vials were enumerated. After 33 hours, we stopped the experiment and measured oxygen concentrations in all vials. No settlers were found on the plastic film under the vial lids. Repeated measures ANOVA was used to analyze the effects of oxygen (high or low) on the cumulative number of settlers per vial at each sampling time. We checked the assumptions of parametric statistics using Cochran's test for homogeneity of variance (Underwood 1997) and the Shapiro-Wilkes test for normality (Zar 1996); the data met these assumptions.

A second *M. manhattensis* experiment (29 September - 4 October, 1999) examined the recovery of larvae following hypoxia. Fifteen replicate high and low-oxygen vials were prepared as described above. Five replicates from each treatment were destructively sampled at the beginning of the experiment to determine starting oxygen concentrations. One day after the experiment started, we counted the number of metamorphosed recruits, measured oxygen concentrations in each vial, then emptied the contents of each vial into a

63 μm sieve. Contents of each sieve were then gently washed into the original vial using oxygenated York River water (filtered through a 10 μm filter), after which vials were resealed. Thus, each vial retained both metamorphosed and remaining unmetamorphosed larvae, and all vials (high and low-oxygen treatments) had high-oxygen water after the first day. Each day for the next 4 days, we counted settlers, measured oxygen, and replaced water and larvae. Repeated measures ANOVA was used to analyze the effects of oxygen (high or low) on the cumulative number of settlers per vial. We only included the data from day 1 (after 24 hours of low oxygen in low-oxygen treatments) and day 5 (after larvae in low-oxygen treatments had been exposed to increased oxygen concentrations for 4 days). We checked the assumptions of parametric statistics using Cochran's test for homogeneity of variance (Underwood 1997) and the Shapiro-Wilkes test for normality (Zar 1996); the data met these assumptions.

Results

Field measurements of recruitment and environmental variables

As predicted from previous studies in the York River (Haas 1977, Kuo and Neilson 1988), hypoxia occurred during neap tides, and was usually more severe downstream. In 1996, hypoxia occurred during at least 3 neap tide deployments, 26-28 June, 22-24 July, and 21-23 August (Fig. 2). During each of these deployments, oxygen downstream fell below 0.5 mg O_2 / L, while oxygen upstream remained above 1 mg O_2 / L (Fig. 2). Oxygen concentrations remained high during spring tides (Fig. 2). Oxygen concentrations during each deployment also varied with the daily tidal cycles, falling during flood tides and briefly rising during ebb tides (Fig. 2). Oxygen data are missing for the first two deployments, 12-14 June (spring tide) and 20-22 June (neap tide).

In 1997, hypoxia occurred during neap tide deployments on 14-16 July and 12-14 August (Fig. 3). For 14-16 July, oxygen concentrations remained hypoxic throughout the

deployment, with lower oxygen levels in the downstream area (Fig. 3). From 12-14 August, we measured hypoxic oxygen concentrations between 1-2 mg O_2 / L downstream during 80% of the deployment, but oxygen remained normoxic upstream (Fig. 3). During some deployments, we only have data from one area of the river (Fig. 3). However, because hypoxia is so well described in the York River (Haas 1977), it may be possible to reconstruct the missing data. For example, during spring tide deployments (25-27 June, 7-9 July, and 6-8 August), oxygen conditions remained largely normoxic, except for a few hours during 6-8 August when oxygen downstream became slightly hypoxic. Because our other deployments (Figs. 2 and 3) show a close relationship during spring tides between oxygen upstream and downstream, and because oxygen is usually lower downstream than upstream (Sisson et al. 1993) it is likely that oxygen in both areas remained largely normoxic during these (25-27 June, 7-9 July, and 6-8 August) spring tide deployments. During the neap tide deployment on 16-18 June, oxygen concentrations upstream remained mostly above 3 mg O_2 / L (Fig. 3). Although we have no data downstream during this deployment, data from other deployments suggest that during neap tides oxygen downstream is generally 0.5 - 1 mg O_2 / L below oxygen concentrations upstream, and therefore we assume that oxygen concentrations downstream remained normoxic during this deployment (16-18 June).

We observed recruitment by all of the sessile epifaunal taxa recently reported as dominant in the York River during a concurrent study (Sagasti et al. in press) (Figs. 4 and 5). These taxa represent 6 phyla and therefore have a variety of larval types and life-history patterns (Table 1). Each taxa showed a distinct seasonal settling pattern, as has been found elsewhere in the Chesapeake Bay system (Abbe 1987). The barnacle *Balanus improvisus* had high recruitment early in 1997, but we recorded only sparse recruitment in 1996, possibly because we missed the late-spring barnacle recruitment. The polychaete *Polydora cornuta* settled early in the summer during both years. Encrusting bryozoans, which we did not identify to species, but which probably included a mixture of two common species,

Conopeum tenuissimum and *Membranipora tenuis* , recruited in July and August each year. Campanularid hydroids, the polychaetes *Sabellaria vulgaris* and *Hydroides dianthus*, and the anemone *Diadumene leucolena* recruited in mid to late summer of both years. *Molgula manhattensis*, a solitary ascidian, recruited throughout the summer of 1997. Although we did not observe *M. manhattensis* recruits in 1996, we did observe adults in other experiments (Sagasti et al. in press), and it is possible that these small, transparent recruits were initially overlooked. For each taxa, the timing of recruitment closely matched the appearance of adults found in a concurrent study (Sagasti et al. in press).

During both years, recruitment for all taxa combined was highest during neap tides in the downstream area, coinciding with hypoxic conditions (Fig 6). In 1996, date, tide and location each had significant effects on recruitment (Table 2), with higher recruitment downstream and higher recruitment during neap tides. During the hypoxic episode on 22-24 June, 1996, recruitment for all taxa combined was 3-6 times higher than during other deployments (Fig. 6). In 1997, date was significant again, and there was a significant tide * location interaction (Table 2). One-factor ANOVAs suggest that the difference between upstream and downstream was most significant during neap tides, and the difference between spring and neap tides was most significant in the downstream location (Table 2). The highest recruitment for all taxa combined in 1997 occurred from August 14-16 (Fig. 6), coinciding with a mild hypoxic episode in the downstream area (Fig. 3).

In both years, many individual taxa (5 of 6 in 1996 and 4 of 8 in 1997) had maximal recruitment during hypoxia (Figs. 4 and 5). For example, in 1996, *Diadumene leucolena*, *Polydora cornuta*, *Sabellaria vulgaris*, encrusting bryozoans and *Hydroides dianthus* had maximum recruitment rates during hypoxia (Fig. 4). *Sabellaria vulgaris* accounted for approximately half of all recruits during the 22-24 June deployment, which had maximum numbers of recruits and coincided with a hypoxic episode. *P. cornuta*, encrusting bryozoans and *H. dianthus* also had high recruitment during this deployment (Fig. 4). All taxa except barnacles recruited successfully during hypoxia.

Statistical results for individual taxa showed that different factors affected recruitment for different taxa (Table 3). In 1996, date had significant effects on recruitment of all taxa analyzed, and both the polychaete *Polydora cornuta* and the anemone *Diadumene leucolena* were significantly more likely to recruit in the downstream, lower oxygen area (Table 3, Fig. 4). Tide had no significant effect on recruitment for the individual taxa analyzed in 1996 (Table 3). The significant increase in total recruitment during neap tide in 1996 appears driven by a single species, the polychaete *Sabellaria vulgaris*, because there was no effect of tide on total recruitment when *S. vulgaris* was eliminated from the analysis (Table 4). However, these results for 1996 could be due to low sample sizes and high variability.

In 1997, when we had more stations and more settling panels per station, patterns for individual taxa were more consistent. Date significantly affected recruitment of encrusting bryozoans, the tunicate *Molgula manhattensis*, the polychaete *Sabellaria vulgaris* and *P. cornuta*, but not campanularid hydroids (Table 3). *S. vulgaris* and *D. leucolena* were each more likely to recruit during neap tides than during spring tides. *S. vulgaris* and *P. cornuta* had significantly higher recruitment in the downstream location (Table 3, Fig. 5). There was a significant interaction between tide and location for barnacles *Balanus improvisus* and campanularid hydroids in 1997 (Table 3). Graphs for these two taxa suggest that recruitment was generally higher during neap tides, and was generally higher in the downstream location, but that the difference between upstream and downstream increased during neap tides (Fig. 5). Overall, for 1997, it appears that 4 of 7 species analyzed had significantly higher recruitment during neap tides (Balanus improvisus, campanularid hydroids, *Sabellaria vulgaris* and *Diadumene leucolena*), and 4 of 7 species analyzed had significantly higher recruitment in the downstream location (*Balanus improvisus*, *Polydora cornuta*, campanularid hydroids, *Sabellaria vulgaris*); none of the taxa analyzed had higher recruitment during spring tides or in the upstream location (Table 3, Fig. 5). In 1997, eliminating Sabellaria vulgaris from the analysis had no effect on

results (Table 4). Thus, it appears that in 1997 significant effects of tide and location on total recruitment were not driven by any single species, but by a range of species.

Larval traps captured a variety of larvae including infaunal and epifaunal species. Because the efficiency of larval traps varied with current speeds, we must interpret trap results cautiously. Traps record which species were available in the plankton, but they do not necessarily reflect larval abundance. The presence of larvae of epifaunal species showed some seasonality (Fig. 7). For example, the anemone *Diadumene leucolena* was present in traps only in mid-late summer during both years (Fig. 7). Overall, larvae of epifaunal species were present during both high and low-oxygen deployments, and were available both upstream and downstream (Fig. 7).

Laboratory experiments: hypoxia effects on recruitment

In all laboratory experiments, low-oxygen vials started with mildly hypoxic conditions (1.44 - 1.54 mg O_2 / L) and ended with near anoxic conditions (0.1 - 0.22 mg O_2 / L) (Table 5), suggesting that during the experiment respiration depleted the water of most of its remaining oxygen. High-oxygen vials started with concentrations above 4 mg O_2 / L but ended with hypoxic oxygen concentrations ranging from 0.7 to 1.64 mg O_2 / L. Therefore, although larvae in high-oxygen vials experienced normoxic (>2 mg O_2 / L) conditions during much of the experiment, they also experienced hypoxia at the end of the experiments. The pH in all vials ranged between 7.51 and 8.10, suggesting that hypercapnia did not occur. There were no significant differences between the number of larvae in hypoxic vs. normoxic treatments at the beginning of experiments (t-tests, $p>0.05$).

We observed recruitment by 5 of 6 taxa which commonly recruited in the field in 1996 and 7 of 8 taxa which commonly recruited in the field in 1997 (Figs. 4, 5 and 8). For each taxa, the seasonal timing of recruitment in the lab experiments was similar to the timing in the field. For example, the polychaete *Polydora cornuta* dominated recruitment during

lab experiments in early July (Fig. 8); in the field it recruited most abundantly in June and July (Figs. 4 and 5).

Seven of 9 taxa that recruited in sufficient numbers for statistical analysis recruited in both high and low-oxygen treatments, but there was a consistent pattern of decreased recruitment in low oxygen for all taxa (Fig. 8). Low oxygen significantly decreased recruitment for 6 of 9 taxa that dominate the epifaunal community in the York River (Table 6), including the polychaetes *Polydora cornuta* and *Hydroides dianthus*, campanularid hydroids, the hydroid *Ectopleura dumortieri*, bryozoans and anemones. We never observed increased recruitment in low relative to high-oxygen treatments.

Laboratory experiments: hypoxia effects on Molgula manhattensis settlement

Settlement of *M. manhattensis* was greater in high-oxygen than in low-oxygen treatments (Table 7, Fig. 9). A significant time * oxygen interaction presumably reflects the increasing difference between time and oxygen treatments over time (Table 7, Fig. 9). Recruitment was similar in high- and low-oxygen treatments for the first few hours. However, in low-oxygen, we observed little or no recruitment after the first 10 hours, while recruitment continued in high-oxygen treatments (Fig. 9). Oxygen concentrations in low-oxygen vials started at approximately 1.5 mg O_2 / L and fell 50% during the experiment to approximately 0.7 mg O_2 / L (Fig. 9). Oxygen remained above 2 mg O_2 / L in high-oxygen vials (Fig. 9).

In the second experiment, which was designed to investigate recovery from hypoxia, low-oxygen conditions caused some larvae to delay settlement until oxygen increased (Fig. 10). Oxygen in low-oxygen vials remained close to 1 mg O_2 / L during the first day of the experiment, while oxygen in high-oxygen treatments remained above 2 mg O_2 / L (Fig. 10). On subsequent days, average oxygen concentrations in both high- and low-oxygen treatments remained above 2 mg O_2 / L (Fig. 10). There was a significant time * oxygen interaction (Table 7), presumably because the difference between treatments decreased with

time (Fig. 10). Recruitment was depressed in low-oxygen treatments after the first day but continued in initially low-oxygen treatments after we raised oxygen levels, until there were no remaining differences between high and low-oxygen treatments (Fig. 10).

Discussion

Although low oxygen decreased recruitment of many York River epifaunal taxa in the laboratory, the largest recruitment pulses in the field occurred during hypoxia. Our laboratory results agree with previous work showing decreased survival and settlement for larvae of oysters, mussels and barnacles in low oxygen (Wang and Widdows 1991, Baker and Mann 1992, Powers et al. in press). However, in our experiments hypoxia did not completely prevent recruitment. Most epifaunal taxa continued to recruit, but at lower densities, during low oxygen in the laboratory, just as they recruited during hypoxia in the field. These results suggest that tolerance of low-oxygen conditions by the larvae of York River epifauna allows them to recruit during hypoxic episodes in both the field and laboratory. Larval tolerance of low oxygen may allow epifaunal communities to persist even though the summer hypoxia season coincides with the recruitment of many epifaunal species.

Differences between laboratory and field conditions

The contrast between hypoxia effects between our laboratory experiments and field patterns suggests that there were important differences between these environments that allow enhanced recruitment of epifauna during hypoxic periods in the field. Environments in the laboratory and the field differ in the timing and severity of hypoxia, the intensity of currents and in the influence of other factors such as tidal stage and larval availability.

In the laboratory, larvae in low-oxygen treatments experienced oxygen concentrations that progressively decreased from mild hypoxia (1.4 mg O_2 / L) to near

anoxia (0.1 - 0.2 mg O_2 / L) (Table 5, Figs. 9 and 10), but in the field, oxygen fluctuated with flood and ebb tides and rarely remained below 0.5 mg O_2 / L longer than a few hours (Figs. 2 and 3). Therefore, larvae in laboratory experiments may have experienced lower oxygen than larvae in the field, and low-oxygen concentrations in the laboratory may have lasted longer than those in the field. Laboratory experiments with the tunicate *Molgula manhattensis* suggest that larvae in the laboratory settled primarily at the beginning of experiments (Fig. 9), when oxygen was relatively high and larvae had not experienced many continuous hours of low oxygen. As Baker and Mann (1992) found for larval oysters, epifaunal taxa in this study may have settled during mild oxygen depletion, but stopped settling as oxygen decreased still further. Settlement may have also decreased due to the length of low-oxygen exposure, which is especially likely if larvae have low energy reserves (Baker and Mann 1992).

Oxygen conditions in the laboratory also differed from those in the field because oxygen concentrations in laboratory low-oxygen treatments remained hypoxic at all times. In the field, during all 3 1996 deployments when hypoxia occurred, and during 1 of 2 1997 deployments when hypoxia occurred, oxygen rose above hypoxic levels at least once. This suggests that, in the field, larvae could have settled preferentially during short periods of high oxygen. As the second experiment with *M. manhattensis* showed, some larvae in our system can delay settlement during hypoxia (Fig. 10), settling after oxygen rises. The ability to delay settlement has also been shown for an infaunal polychaete, *Paraprionospio pinnata* (Powers et al. in press), and other species of bivalves, fish and insects (Widdows et al. 1991; Keckies et al. 1996; Nebeker et al. 1996). Thus, delaying development or settlement may be a general strategy used by animals in areas with fluctuating oxygen conditions.

Another difference between the laboratory and the field is the current regime. Laboratory experiments occurred in stagnant conditions, whereas in the field current speeds during hypoxic episodes can reach 40 cm / s (Sisson et al. 1991). Therefore, larvae in the

field likely had a constant stream of water flowing over their bodies, enhancing the flux of oxygen by reducing the thickness of diffusive sublayers. Stagnant conditions may have decreased the flux of oxygen to larvae in the laboratory by allowing a buildup of thick diffusion sublayers.

Unlike larvae in laboratory experiments, larvae in the field were also subject to many factors besides hypoxia that can be expected to influence recruitment. In the York River, hypoxia is correlated with neap tides and lower current speeds (Haas 1977); each of these factors may have changed recruitment. Many animals coordinate spawning or recruitment with tidal stages (Seitz and Schaffner 1995; Robertson et al. 1999), and it is possible that epifaunal species in the York River prefer to settle during neap tides for reasons unrelated to hypoxia. For most epifaunal species in the York River, little is known about the timing of reproduction (Table 1). Larval traps showed that, although their relative abundances may differ, larvae of most epifaunal species are available during neap and spring tides. For the few epifaunal species in this system for which literature is available about the timing of reproduction, there is no suggestion that neap/spring cycles influence settlement (Table 1). For example, larval availability of the polychaete *Polydora cornuta* does not fluctuate with spring/neap tides (Orth 1971), yet *P. cornuta* showed high settlement during neap tides in the field (Figs. 4 and 5). This suggests that for some species, increased recruitment during hypoxia is not caused by neap/spring cycles in larval availability.

Hypoxia in the field is also correlated with decreased tidal currents (Haas 1977, Sisson et al. 1991) which could influence recruitment. The lower York River is dominated by tidal currents with maximum speeds of 40-50 cm s^{-1} during spring tides and 20-40 cm s^{-1} during neap tides (Sisson et al. 1991). Fast currents can sweep invertebrate larvae away from potential settling surfaces (Eckman 1983), decreasing settlement. This effect has been noted for a wide variety of invertebrates (Eckman 1983; Pawlik and Butman 1993; Leonard et al. 1998). Recruitment of epifaunal species in the York River may increase during neap tides because slower currents allow more larvae to reach settling substrates and attach. In

the future, this hypothesis could be tested in the upper water column, where hypoxia does not occur.

Our field results contrast greatly with those of a similar study (Powers et al. in press) in the Gulf of Mexico. In that study, barnacle cyprids and other plankton avoided hypoxic locations, leading to decreased recruitment in hypoxic areas. Major differences between physical conditions in the York River Estuary and those of the Gulf of Mexico include differences in currents and differences in the timing and severity of oxygen depletion. In the York River, tidal currents maintain continuous water movement, but in the Gulf of Mexico water currents are relatively weak (Powers et al. in press). Oxygen concentrations in the Gulf of Mexico can continuously remain below 0.1 mg O_2 / L for 2-3 weeks at a time (Powers et al. in press), but hypoxia in the York River is milder and rarely lasts more than a week. It seems likely that the ability of benthic communities to exist in hypoxic areas decreases as currents decrease, oxygen concentrations fall, and low oxygen conditions become more persistent.

Differences in duration of hypoxia between the York River and the Gulf of Mexico could also result in different strategies by larvae. In the York River, where hypoxic episodes last a week or less, high recruitment during hypoxia could be explained by the ability of larvae to delay settlement and metamorphosis. If larvae can delay settlement during hypoxia, this could increase the abundance of competent larvae that are ready to set, triggering high recruitment when oxygen increases. High recruitment could occur during a hypoxic event if the settlement occurred in an oxic window within a hypoxic period. In contrast, larvae in the Gulf of Mexico, where low-oxygen episodes last several weeks, might have a higher likelihood of death while delaying settlement (but at least one species in the Gulf of Mexico, the polychaete *Paraprionospio pinnata*, does delay settlement for over a week) (Powers et al. in press). A more successful strategy in the Gulf of Mexico may be to avoid hypoxic water masses (Powers et al. in press).

Seasonal timing of recruitment

A key factor that influenced recruitment of some epifaunal taxa was seasonal changes in larval availability. Larval traps showed distinct seasonal peaks in the abundance of larvae for several species (Fig. 7), and these peaks coincided with recruitment in the field (Figs. 4 and 5). For example, *Diadumene leucolena* recruited only in mid-summer (Figs. 6 and 7) when its larvae were available (Fig. 7). The polychaete *Polydora cornuta* was available throughout the summer, but appeared more abundant early in the summer (Fig. 7); this species showed a similar seasonal pattern of recruitment, settling on panels in greatest abundance in June and July but continuing to settle throughout the summer during both 1996 and 1997 (Figs. 4 and 5). In contrast, barnacle larvae were present throughout the summer of both years (Fig. 7), yet few barnacles settled in mid-summer (Figs. 4 and 5). We did not collect the larvae of other epifaunal taxa, such as campanularid hydroids, possibly because these species are easily damaged during processing. Abundance differences in larval traps between 1996 and 1997 may reflect the different sieve sizes used in processing, with increased retention of larvae in 1997 when a smaller sieve size was used.

Community effects

In this study, the larvae of most epifaunal taxa showed similar responses to hypoxia, suggesting that the observed levels of oxygen stress do not impact the relative recruitment success of different species. For example, 6 of 9 taxa in laboratory experiments had significantly higher recruitment in high oxygen, with 2-3 times more recruitment in high oxygen than in low oxygen (Fig 8). The remaining taxa all showed a consistent trend of higher recruitment in high-oxygen (Fig 8). In the field, all taxa recruited during hypoxia, except for barnacles (*Balanus improvisus*) and serpulids (*Hydroides dianthus*) in 1997, which recruited before and after the major hypoxic events (Fig. 5), suggesting that most taxa are at least somewhat tolerant of low oxygen. Therefore, the effect of hypoxia on recruitment may not have strong effects on interactions between species in this community.

Estuarine animals are often adapted to a variety of stresses (Levinton 1982), thus, it may not be surprising that species interactions are not greatly influenced by physical disturbance.

In conclusion, physiological stresses such as hypoxia can have important effects on recruitment, but the net effects of these stresses may be difficult to predict since regional-scale stresses are often correlated with other environmental factors. In our laboratory experiments, hypoxic stress decreased recruitment of the larvae of dominant epifaunal taxa. This decrease in recruitment depended on the severity and duration of oxygen depletion. In one species studied experimentally (*Molgula manhattensis*) settlement resumed after hypoxic stress stopped. Despite negative effects of hypoxia on recruitment, periodic hypoxia had no detectable negative effect on recruitment of York River epifaunal species in the field, and this high tolerance may allow species to persist in areas where hypoxia coincides with recruitment.

Acknowledgments

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Table 1. Early life histories of dominant epifaunal invertebrates in the York River, Chesapeake Bay, USA. A = Anthozoa, B = Bryozoa, C = Crustacea, H = Hydrozoa, P = Polychaeta, T=Tunicata.

Species	Larval type	Time in Plankton	Spring/neap cycle in larval availability or settlement?
Balanus improvisus (C)	nauplius and cyprid (Doochin 1951)	1-2 weeks for *Balanus eburneus* (Costello et al. 1957)	no (McDougall 1943)
Conopeum tenuissimum (B)	cyphonautes (Cook 1962)	more than 5 days (possibly weeks) (Cook 1962)	no (Dudley 1973)
Diadumene leucolena (A)	planula (Spaulding 1974)	unknown	unknown
Ectopleura dumortieri (H)	hydromedusa (Calder 1971)	unknown	no for *Tubularia crocea* (McDougall 1943)
Hydroides dianthus (P)	trochophore (Zeleny 1905)	2 weeks (Zeleny 1905)	no for *Hydroides hexagonous* (McDougall 1943)
Membranipora tenuis (B)	cyphonautes (Ryland 1974)	unknown	unknown
Molgula manhattensis (T)	tadpole (Berrill 1931)	1 day (Costello et al. 1957)	unknown
Obelia bicuspidata (H)	hydromedusa (Calder 1971)	up to 2 months for other *Obelia* species (Costello et al. 1957)	unknown
Polydora cornuta (P)	trochophore (Blake 1969)	weeks-varies greatly with temperature (Blake 1969)	no (Orth 1971)
Sabellaria vulgaris (P)	trochophore (Curtis 1978)	1-2 months (Curtis 1978)	no (McDougall 1943; Curtis 1978)

Table 2. ANOVA results for recruitment in the field in (a) 1996 and (b) 1997. Factors were date, tide (neap or spring) and location (upstream or downstream). The response variable was the log transformed number of recruits $m^{-2} \cdot$ day for all species combined. Because time is considered a blocking factor, we have not estimated the interaction terms involving time. One factor ANOVAs in b were conducted to investigate a significant tide*location interaction.

a. 1996

Source	DF	SS	MS	F	P	% variance
date	4	15.001	3.750	28.44	<0.001	50.5
tide	1	0.554	0.554	4.20	0.043	1.8
location	1	0.633	0.633	4.80	0.031	2.1
tide*location	1	0.054	0.054	0.41	0.524	0.1
error	103	13.582	0.132			45.3
total	110					

b. 1997

Source	DF	SS	MS	F	P	% variance
Three factor ANOVA						
date	3	16.698	5.566	44.33	<0.001	42.1
tide	1	5.552	5.552	44.22	<0.001	12.2
location	1	3.340	3.340	26.60	<0.001	8.3
tide*location	1	1.344	1.344	10.71	0.001	3.1
error	120	15.065	0.126			34.3
total	126					
One factor ANOVA - only spring tide						
location	1	0.322	0.322	3.39	0.071	
error	58	5.502	0.095			
One factor ANOVA - only neap tide						
location	1	6.354	6.354	15.73	< 0.001	
error	65	26.261	0.404			
total	66	32.615				
One factor ANOVA - only upstream						
tide	1	0.647	0.647	1.92	0.170	
error	69	23.209	0.336			
total	70	23.856				
One factor ANOVA - only downstream						
tide	1	6.029	6.029	38.06	< 0.001	
error	54	8.553	0.158			
total	55	14.582				

Table 3. Results of ANOVAs for recruitment of individual taxa in the field in (a) 1996 and (b) 1997. Factors were date, tide (neap or spring) and location (upstream or downstream). The response variable was the number of recruits $m^{-2} \cdot$ day or the log transformed number of recruits / $m^2 \cdot$ day. Because time is considered a blocking factor, we have not estimated the interaction terms involving time. For each taxa, we considered only dates where average recruitment in at least one location during neap or spring tide was at least equal to 10% of the maximum recruitment. For some taxa, we could meet the assumptions of ANOVA even after transformation and no analyses were performed.

a. 1996

Source	DF	SS	MS	F	P
Polydora cornuta 14 June - 2 August					
date	2	3.895	1.948	14.97	0.000
tide	1	0.231	0.231	1.78	0.187
location	1	1.019	1.019	7.83	0.007
tide*location	1	0.345	0.345	2.65	0.108
Error	66	8.588	0.130		
Total	71				
Encrusting bryozoans 24 July - 29 August					
date	2	0.711	0.355	11.85	0.000
tide	1	0.064	0.064	2.14	0.149
location	1	0.039	0.039	1.30	0.259
tide*location	1	0.118	0.118	3.95	0.052
Error	55	1.650	0.030		
Total	60				
Campanularid hydroids 24 July - 29 August					
date	2	3.712	1.856	15.16	0.000
tide	1	0.251	0.251	2.05	0.158
location	1	0.085	0.085	0.69	0.408
tide*location	1	0.015	0.015	0.13	0.725
Error	55	6.736	0.123		
Total	60				

Diadumene leucolena 24 July - 29 August					
date	2	6.030	3.015	39.14	0.000
tide	1	0.076	0.076	0.99	0.324
location	1	0.454	0.454	5.89	0.018
tide*location	1	0.028	0.028	0.36	0.552
Error	55	4.237	0.077		
Total	60				

b. 1997

Source	DF	SS	MS	F	P
Balanus improvisus 18 June - 27 June					
tide	1	0.477	0.477	3.29	0.080
location	1	3.988	3.988	27.54	0.000
tide*location	1	3.315	3.315	22.89	0.000
Error	28	4.055	0.145		
Total	31				
Polydora cornuta 18 June - 14 August					
date	2	2.304	1.152	12.74	0.000
tide	1	0.024	0.024	0.27	0.608
location	1	0.417	0.417	4.61	0.035
tide*location	1	0.010	0.010	0.11	0.738
Error	89	8.050	0.090		
Total	94				
Campanularid hydroids 9 July - 12 September					
date	2	4.480	2.240	0.41	0.663
tide	1	116.684	116.684	21.50	0.000
location	1	81.011	81.011	14.93	0.000
tide*location	1	34.775	34.775	6.41	0.013
Error	89	483.046	5.427		
Total	94				

Encrusting bryozoans 9 July - 12 September					
date	2	0.185	0.093	3.53	0.033
tide	1	0.012	0.012	0.47	0.493
location	1	0.050	0.050	1.92	0.170
tide*location	1	0.001	0.001	0.04	0.842
Error	89	2.335	0.026		
Total	94				
Molgula manhattensis 18 June - 12 September					
date	3	1.157	0.386	5.93	0.001
tide	1	0.124	0.124	1.91	0.169
location	1	0.084	0.084	1.29	0.258
tide*location	1	0.029	0.029	0.44	0.507
Error	120	7.801	0.065		
Total	126				
Sabellaria vulgaris 9 July - 9 September					
date	2	18.077	9.038	108.93	0.000
tide	1	4.131	4.131	49.79	0.000
location	1	0.503	0.503	6.06	0.016
tide*location	1	0.002	0.002	0.02	0.877
Error	89	7.384	0.083		
Total	94				
Diadumene leucolena 8 August - 14 August					
tide	1	5.181	5.181	41.28	0.000
location	1	0.019	0.019	0.15	0.702
tide*location	1	0.101	0.101	0.81	0.377
Error	27	3.389	0.126		
Total	30				

Table 4. ANOVA results for total recruitment minus *Sabellaria vulgaris* in the field in (a) 1996 and (b) 1997. Factors were date, tide (neap or spring) and location (upstream or downstream). The response variable was the log transformed number of recruits $m^{-2} \cdot$ day for all species other than *Sabellaria vulgaris* combined. Because time is considered a blocking factor, we have not estimated the interaction terms involving time.

1996.

Source	DF	SS	MS	F	P
date	4	13.420	3.355	37.82	0.000
tide	1	0.001	0.001	0.00	0.952
location	1	0.779	0.779	8.78	0.004
tide*location	1	0.047	0.047	0.53	0.469
error	103	9.138	0.089		
total	110				

b. 1997

Source	DF	SS	MS	F	P
date	3	15.342	5.114	40.21	0.000
tide	1	4.990	4.990	39.23	0.000
location	1	3.581	3.581	28.15	0.000
tide*location	1	1.617	1.617	12.71	0.001
error	120	15.263	0.127		
total	126				

Table 5. Oxygen concentrations (mg O_2 / L) in low- and high-oxygen treatments before and after laboratory recruitment experiments.

Date	Low-oxygen treatment (mean (st. dev)).		High-oxygen treatment (mean (st. dev)).	
	Before (n=5)	After (n=20)	Before (n=5)	After (n=20)
July 8-9, 1999	1.4 (0.1)	0.2 (0.2)	4.9 (0.1)	0.9 (0.5)
July 15-16, 1999	1.4 (0.2)	0.2 (0.03)	4.5 (0.2)	1.6 (0.6)
July 29-30, 1999	1.5 (0.2)	0.2 (0.2)	4.4 (0.2)	1.1 (0.7)
Aug 29-30, 1999	1.5 (0.3)	0.1 (0.1)	4.4 (0.1)	0.7 (0.5)

Table 6. Statistical results for effects of oxygen treatment (high- vs. low-oxygen) on the number of recruits in laboratory experiments. We did a separate analysis for each taxa that recruited in at least 2 vials in each experiment. P-values are from Mann-Whitney U-tests except where noted (**), in which case they are from 1-sample t-tests. For taxa with recruitment in multiple experiments, we pooled p-values to get one p-value for each species. Significant results are marked with an asterisk.

Species	31 June - 1 July	8-9 July	15-16 July	29-30 July	29-30 August	pooled p-values, X2
	Test Statistic, P	Test Statistic, P	Test Statistic, P	Test Statistic, P	Test Statistic, P	Test Statistic, P
Polydora cornuta	71.5, 0.0102	237.5, <0.0001	255.0, <0.0001	317.5, 0.0015	410.0, 1.0000	59.0, <0.0001*
Molgula manhattensis	96.0, 0.5019	386.0, 0.3999	430.0, 0.3939	313.5, 0.0049	390.0, 0.3939	17.6, 0.0625
Campanularid hydroids	1.5**, 0.1679	370.0, 0.1231	366.0, 0.1784	235.0, <0.0001	247.5, <0.0001	45.6, <0.0001*
Nereis succinea		399.5, 0.5536				
Hydroides dianthus		1.453**, 0.1625	329.0, 0.0039			14.7, 0.0053*
Bryozoans			359.0, 0.0387*			
Anemones				379.0, 0.1508	309.0, 0.0033	15.2, 0.0043*
Barnacles				410.0, 1.0000		
Ectopleura dumortieri					302.5, 0.0028*	

Table 7. Results of *Molgula manhattensis* laboratory recruitment experiments. (a) Repeated Measures ANOVA for first experiment testing course of response to hypoxia. Factors were oxygen (hypoxic or normoxic) and time, and the response variable was the cumulative number of recruits per vial at each sampling time. (b) Repeated Measures ANOVA for second experiment testing recovery from hypoxic conditions. Analysis as in (a).

a. Timing of Recruitment, *Molgula manhattensis*

Source	DF	SS	MS	F	P
Within Subjects					
Time	8	20898.54	2612.32	72.22	0.0001
Time* Oxygen	8	3225.90	403.23	11.15	0.0001
Error	144	5208.44	36.17		
Between Subjects					
oxygen	1	3458.45	3458.45	8.58	0.0090
Error	18	7259.65	403.31		

b. Recovery from hypoxia, *Molgula manhattensis*

Source	DF	SS	MS	F	P
Within Subjects					
Time	1	608.4	608.4	12.17	0.0026
Time* Oxygen	1	547.6	547.6	10.95	0.0039
Error	18	900	50		
Between Subjects					
oxygen	1	1276.9	1276.9	4.61	0.0457
Error	18	4988.6	277.1		

Fig. 1. Sampling stations in the York River, Virginia. Locations were chosen randomly along the 15 m depth contour.

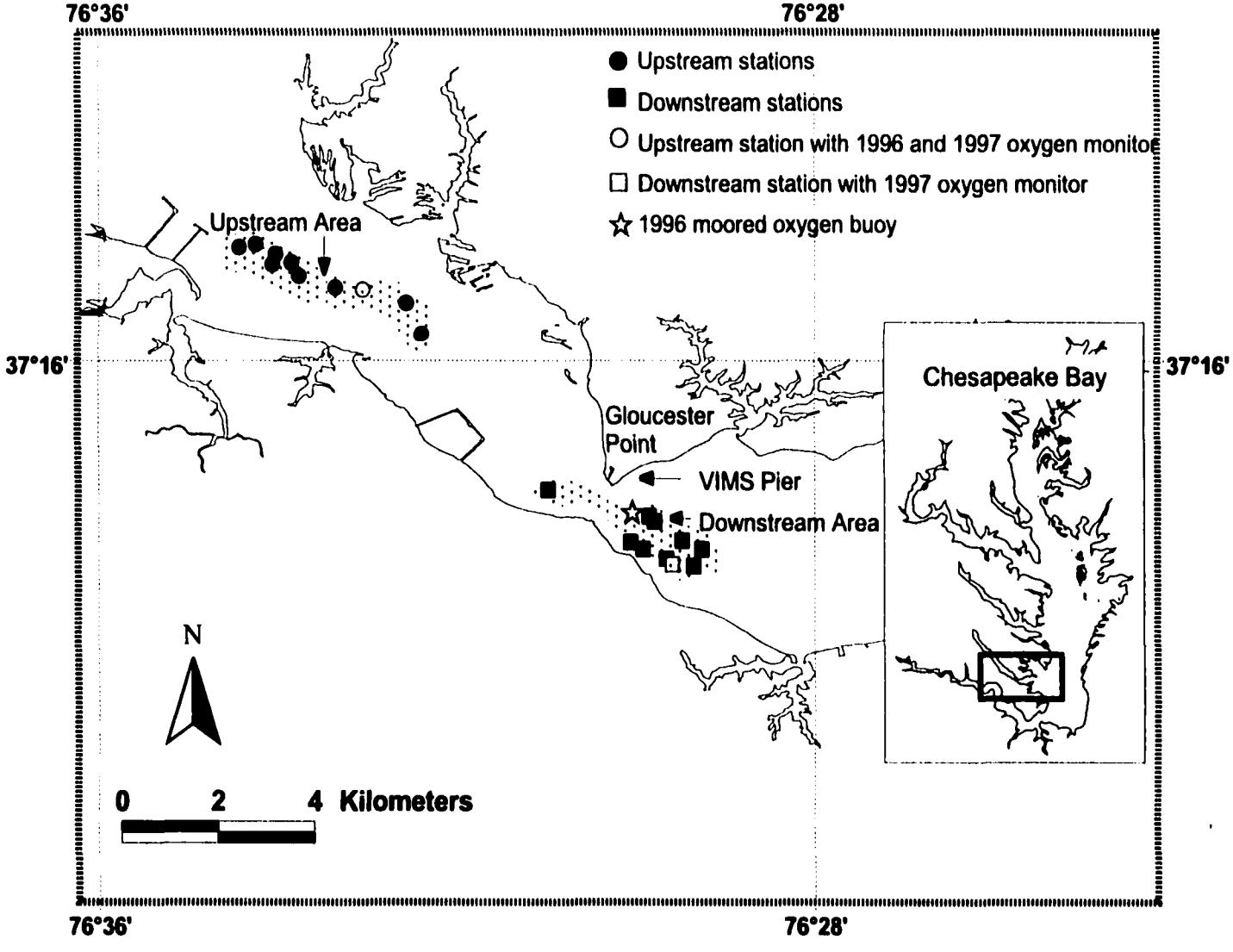


Fig. 2. Hourly dissolved oxygen concentrations at upstream and downstream monitor (14.5 m deep) during 1996 deployments. All oxygen concentrations below the dashed reference line (2 mg O_2 / L) were considered hypoxic.

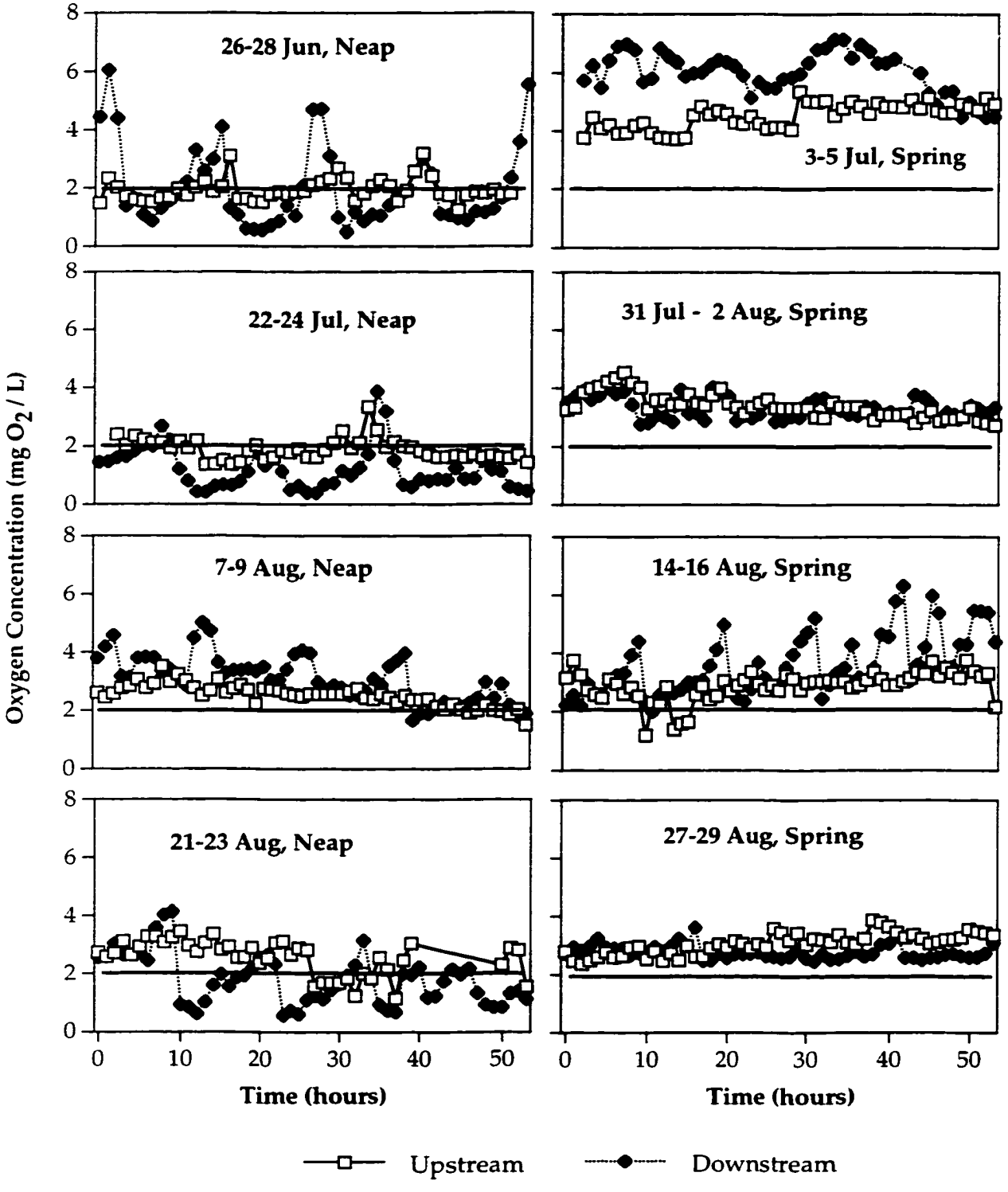


Fig. 3. Hourly dissolved oxygen concentrations at upstream and downstream monitor (14 m deep) during 1997 deployments. All oxygen concentrations below the dashed reference line (2 mg O_2 / L) were considered hypoxic.

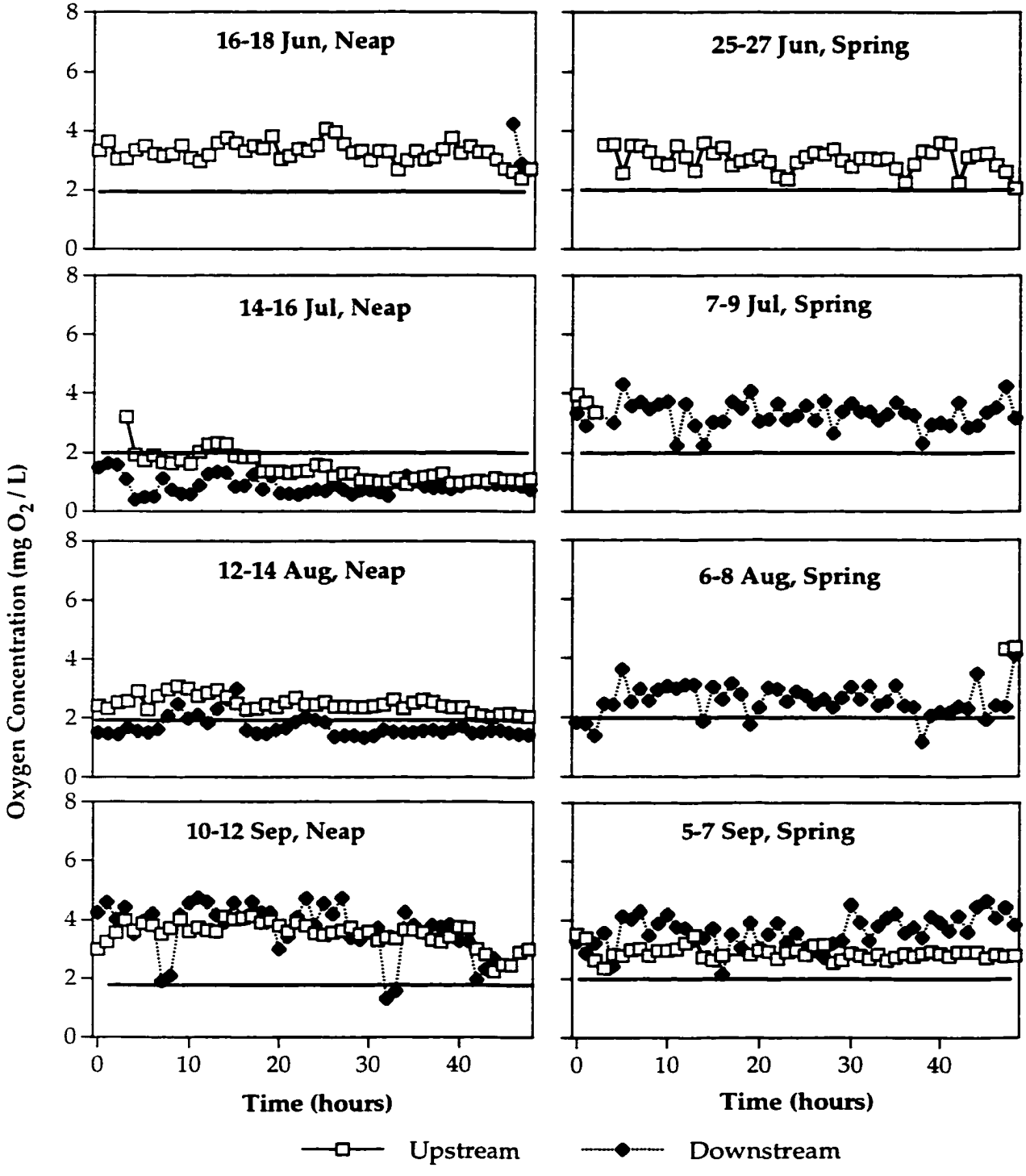


Fig. 4. Recruitment (mean ± 1 standard error) of common taxa during 1996 deployments. Shaded regions denote periods during which hypoxia occurred. Note variation in scales of vertical axes.

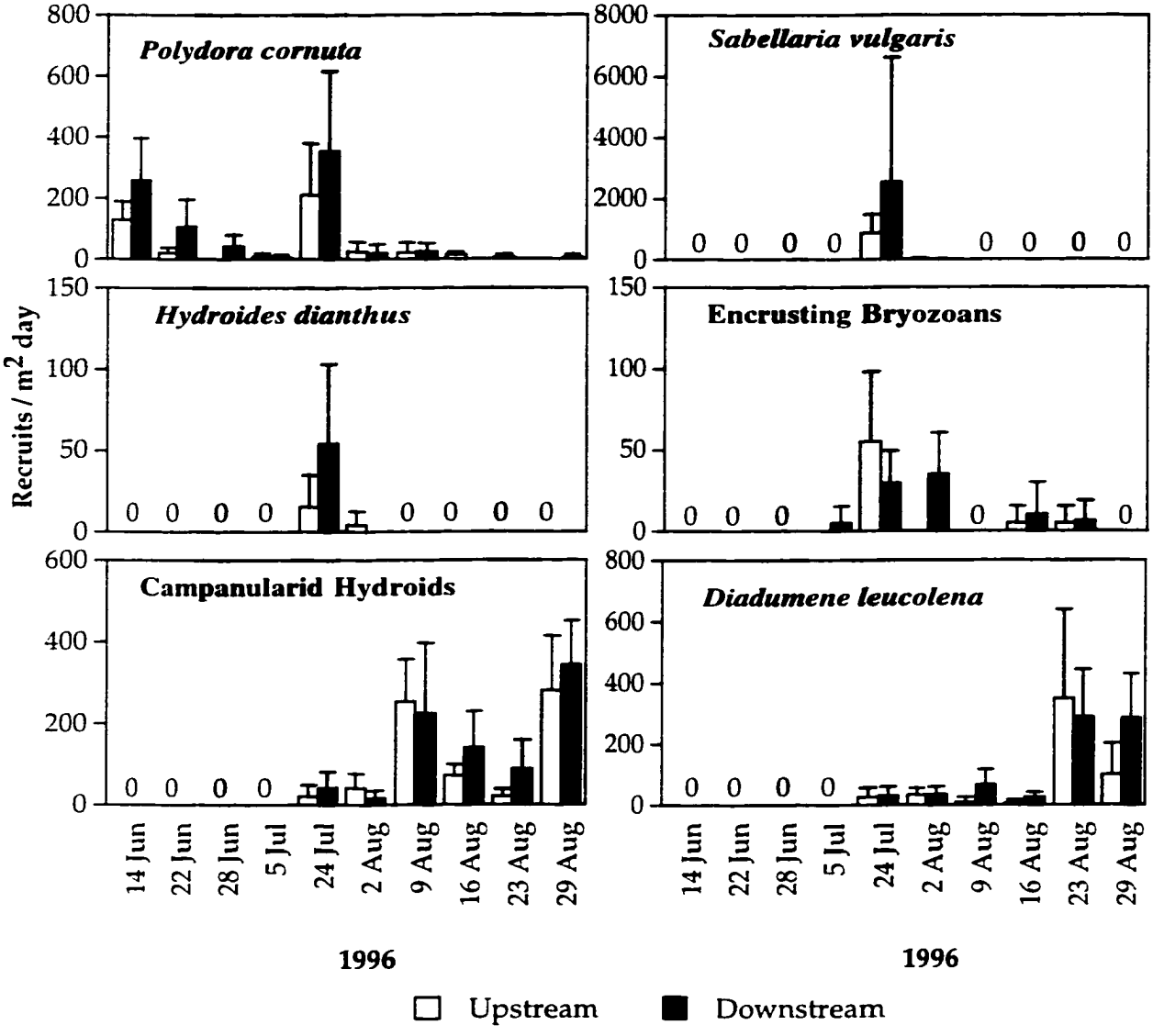


Fig. 5. Recruitment (mean ± 1 standard error) of common taxa during 1997 deployments. Shaded regions denote periods during which hypoxia occurred. Note variation in scales of vertical axes.

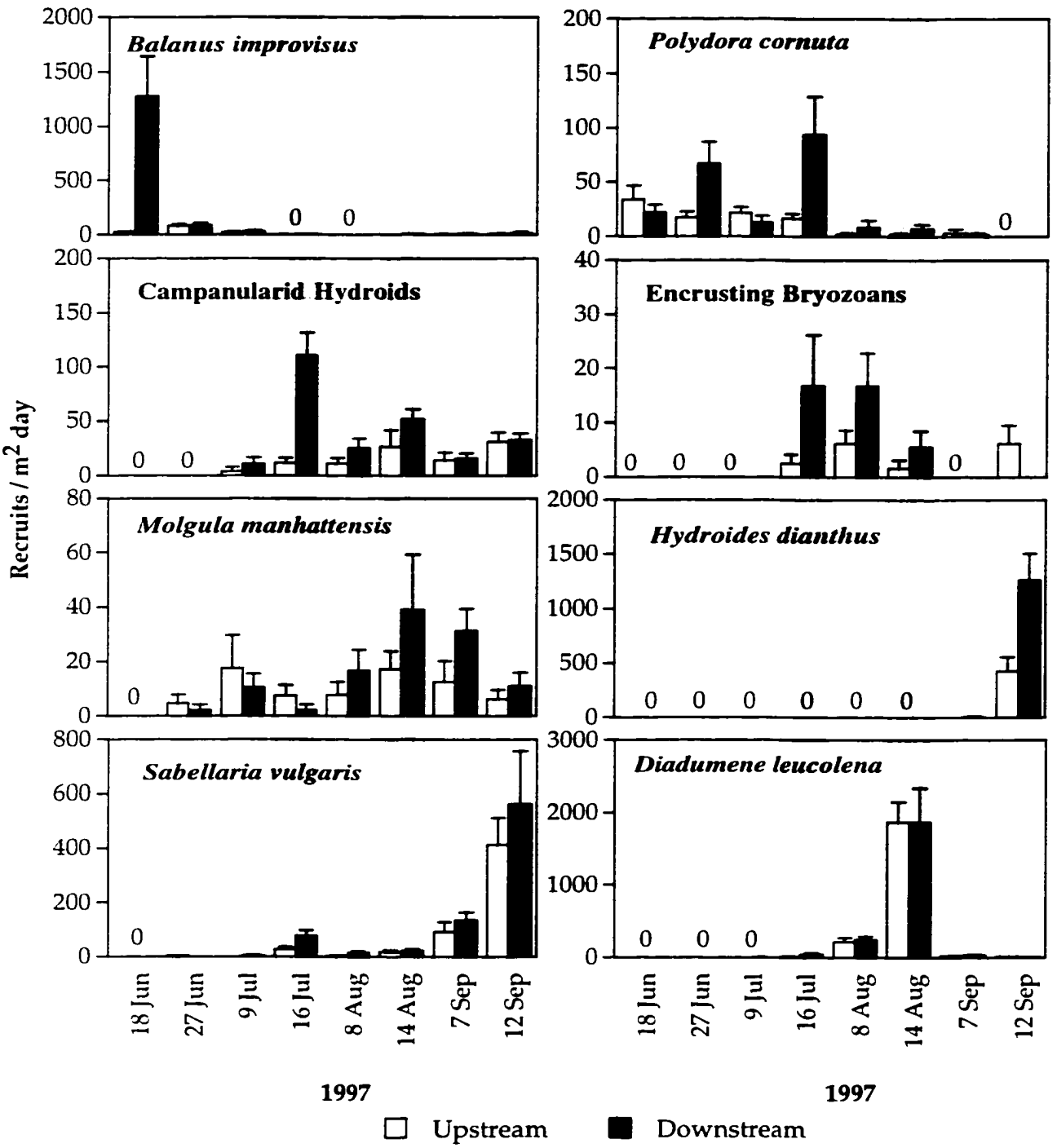
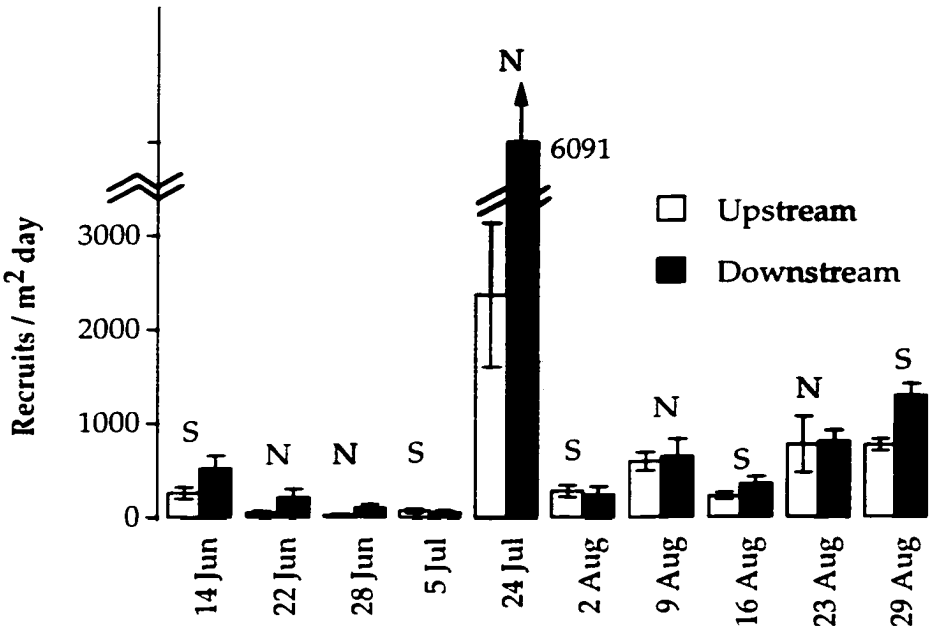
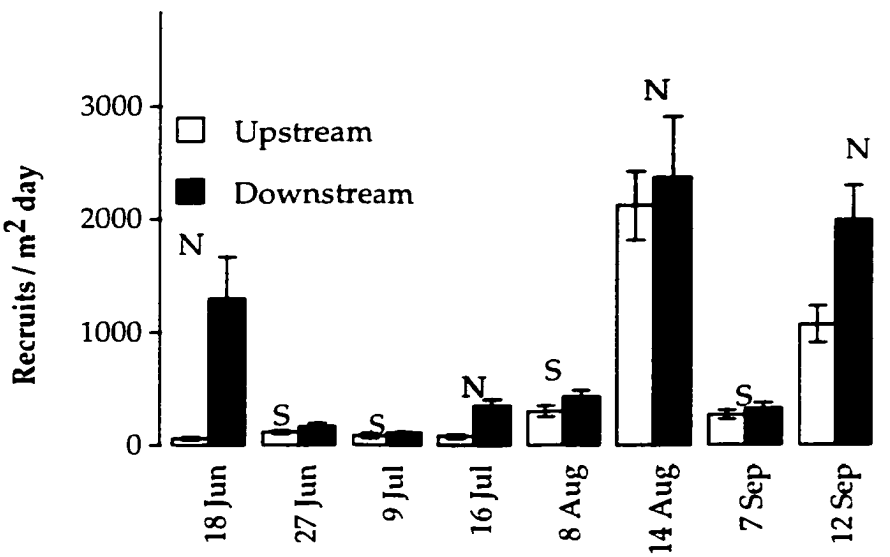


Fig. 6. The combined recruitment (mean ± 1 standard error) of all taxa in (a) 1996 and (b) 1997 during spring tides (S) or neap tides (N). Shaded regions denote periods during which hypoxia occurred. Note the break in the y-axis above 3000 recruits/ m^2 day in 1996.



1996



1997

Fig. 7. Abundance (mean ± 1 standard error) of larvae of epifaunal taxa caught in larval traps during deployments in 1996 and 1997. Shaded regions denote periods during which hypoxia occurred. Samples sizes (n) showing the number of traps processed for each deployment are noted at the bottom for each sampling period (upstream, downstream). Note variation in scales of vertical axes.

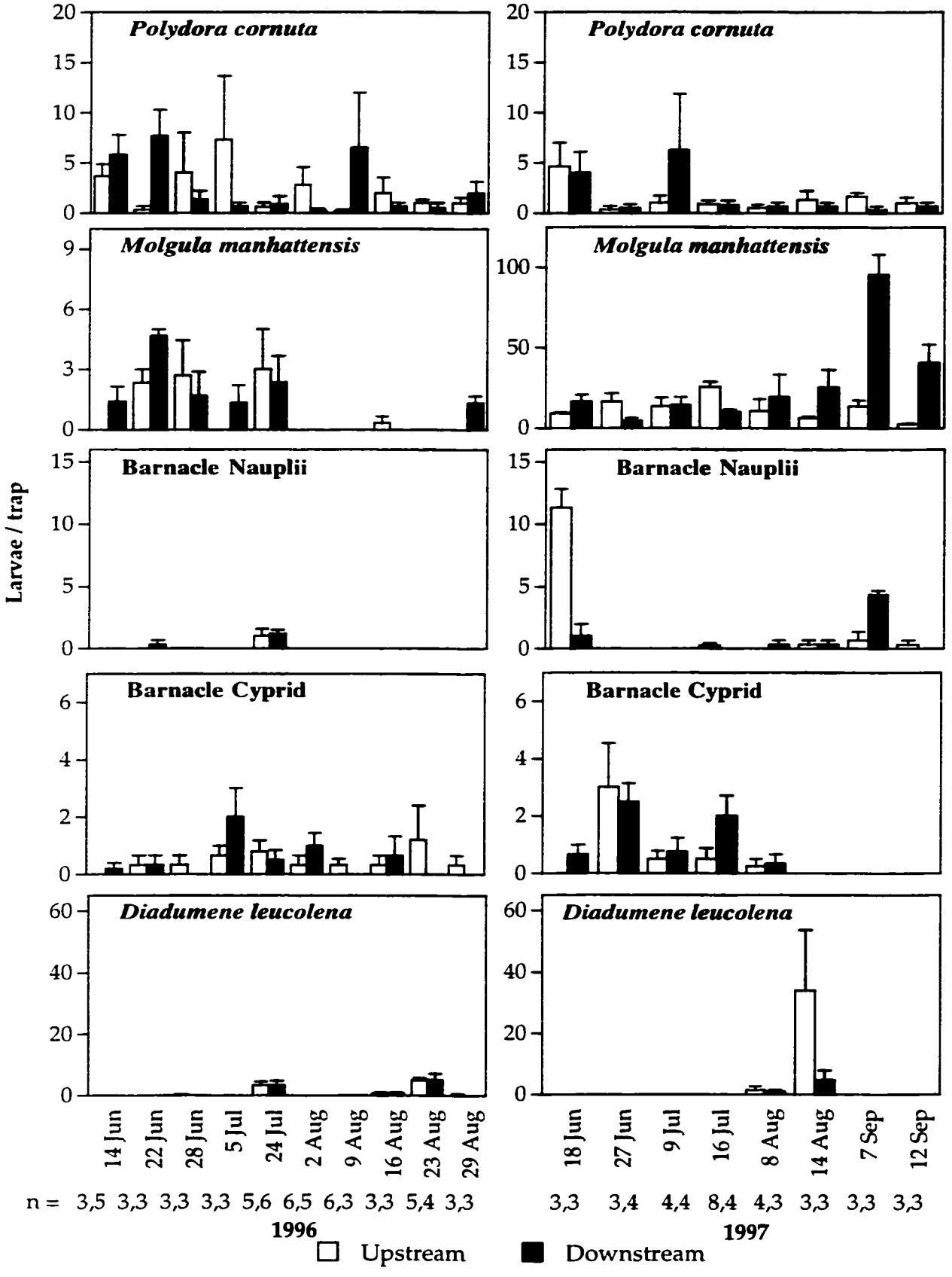


Fig. 8. Recruitment (mean ± 1 standard error) of epifaunal taxa during laboratory experiments in 1999.

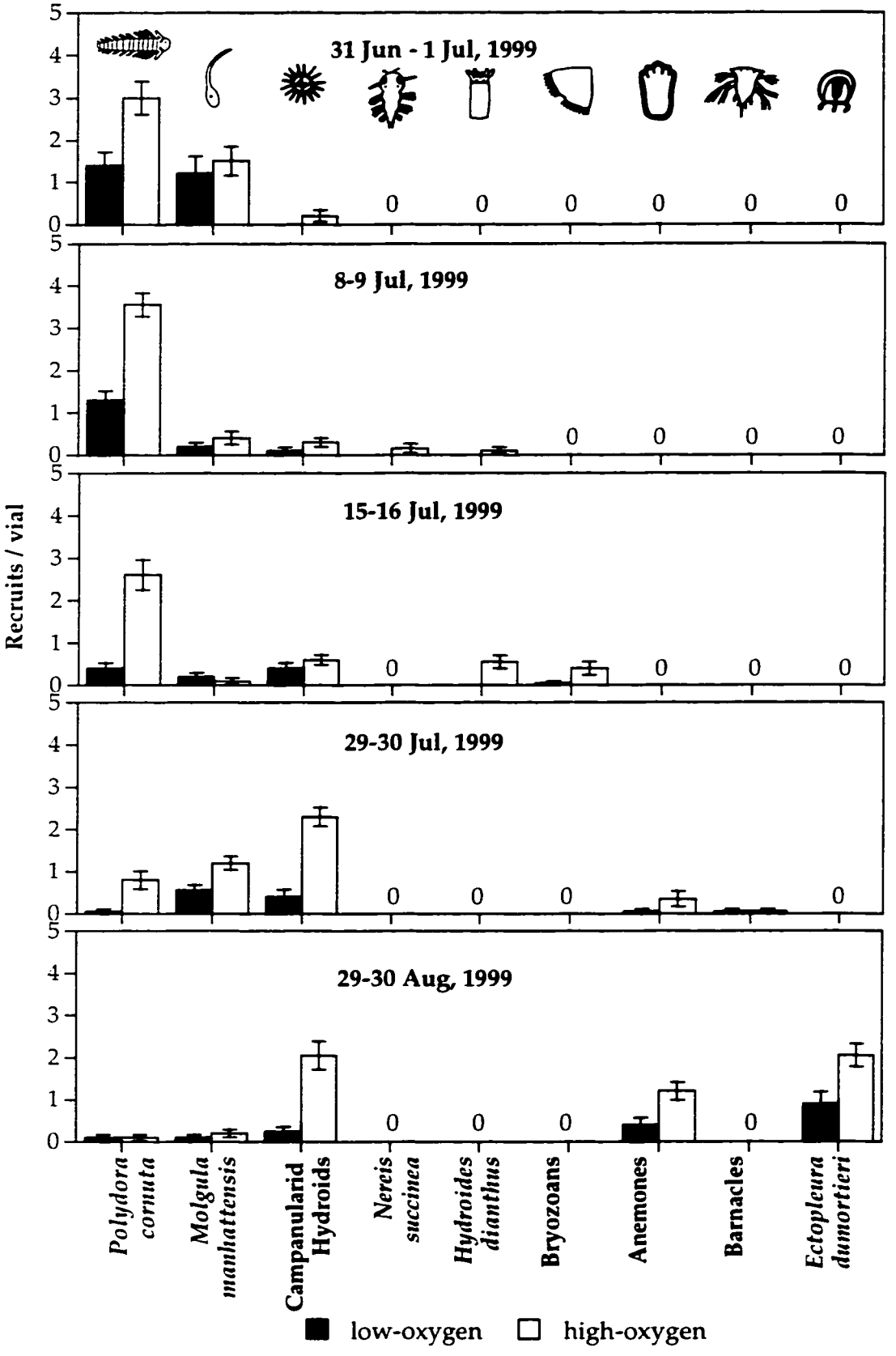


Fig. 9.

a. Recruitment (mean ± 1 standard error) of *Molgula manhattensis* during timing of recruitment experiment on 8-9 June, 1999.

b. Dissolved oxygen concentration (mean ± 1 standard error) in vials at the before and after timing of recruitment experiment on 8-9 June, 1999.

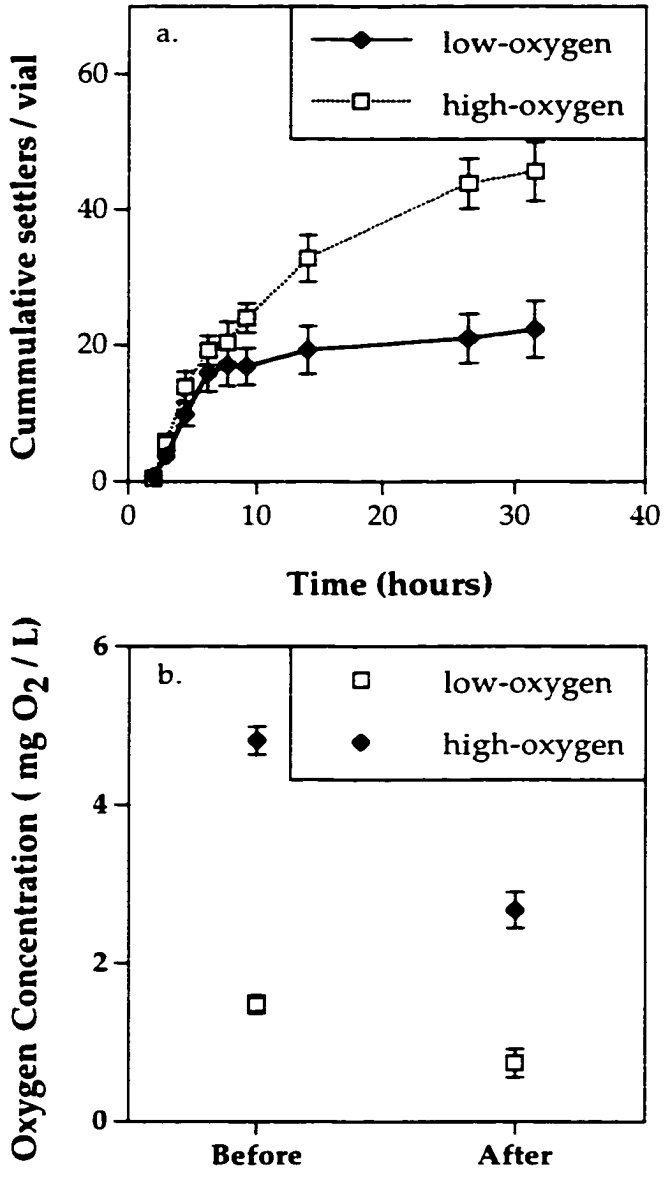
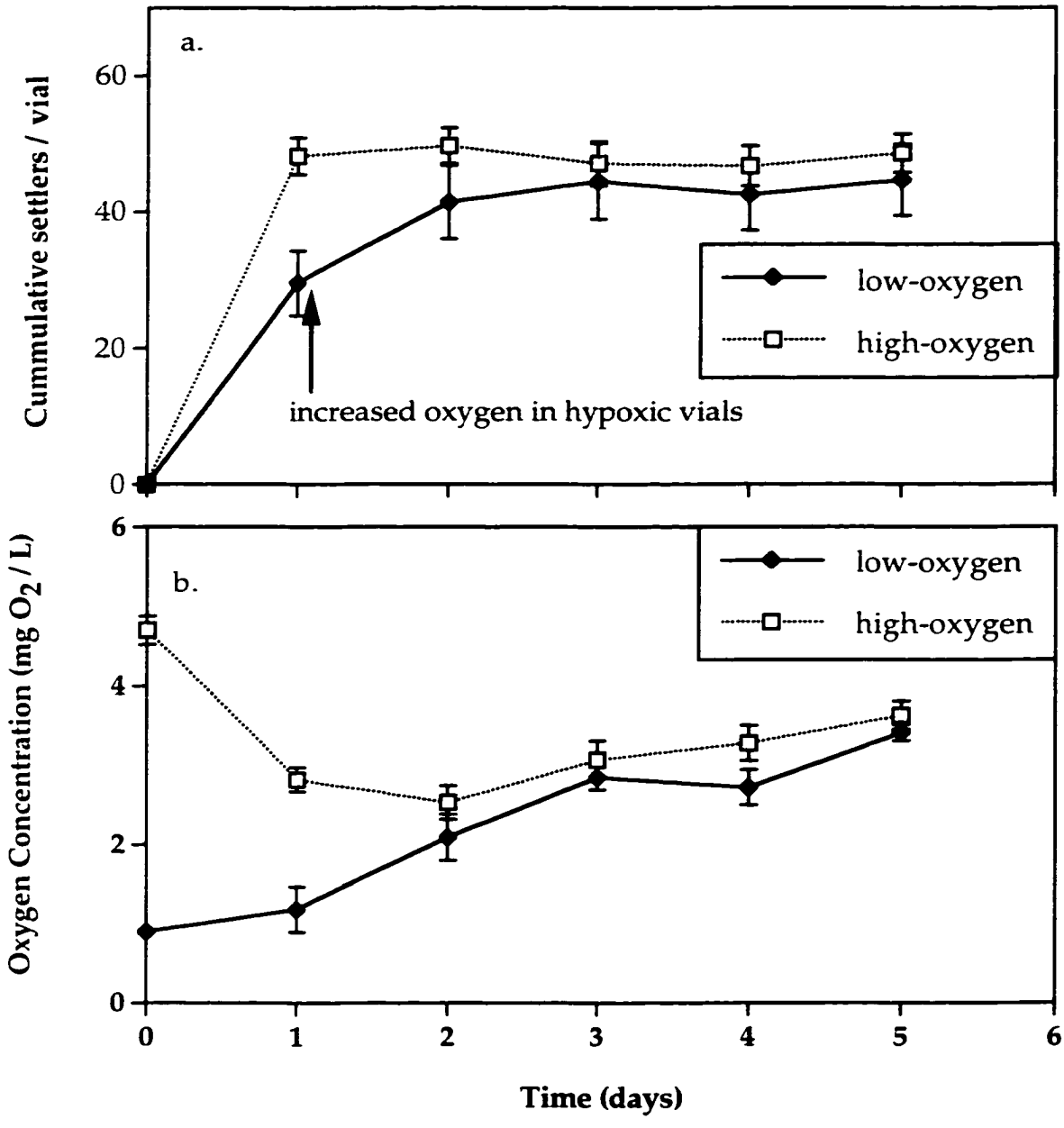


Fig. 10.

a. Recruitment (mean ± 1 standard error) of *Molgula manhattensis* during recovery from hypoxia experiment on 29 September - 4 October, 1999. The arrow marks the time when oxygen concentrations were increased to high levels in low oxygen treatments.

b. Dissolved oxygen concentration (mean ± 1 standard error) in vials each day during recovery from hypoxia experiment on 29 September - 4 October, 1999.



CHAPTER 4: COMPETITION IN THE YORK RIVER EPIFAUNAL COMMUNITY

Introduction

Competition is a major factor that structures communities, because it can change species distributions (Connell 1961, Fenchel 1975, Hacker and Bertness 1999) and lead to low diversity communities (Connell 1978, Menge and Sutherland 1987). Many factors, including competitive networks (Jackson 1977), variable recruitment (Dayton 1971, Sutherland 1978, Sutherland and Ortega 1986), and predation (Lubchenco 1978, Sutherland and Ortega 1986) can prevent competitive exclusion. Stress and physical disturbance also modify resources or decrease growth rates, changing the rate, significance and outcome of competitive interactions (Lubchenco 1978, Petraitis and Dudgeon 1999) and varying the importance of competition (Connell 1978, Huston 1979, Menge and Sutherland 1987).

Competition is often intense in hard-substrate communities, because space for attachment is often limiting (Connell 1961, Dayton 1971, Osman 1977 but see Brown and Swearingen 1998). Sessile epifaunal species compete by capturing space and preventing others from invading it (Sutherland and Karlson 1977, Breitburg 1985), or by overgrowing and smothering other species (Jackson 1979, Buss 1979). Some species capture and retain space more efficiently than others, resulting in competitive hierarchies (Dayton 1971, Osman 1977, Barnes and Clark 1995 but see Sutherland and Karlson 1977 and Buss and Jackson 1979). Competitive ability depends on growth form (Jackson 1979, Buss 1979), whether species are colonial or solitary (Jackson 1977, Buss 1979), and age, size or developmental stage (Sutherland 1981). Good competitors often grow quickly, allowing them to displace others (Huston 1979), but many good competitors also have low tolerance

for stress (Grime 1973). Some epifaunal species may avoid being excluded by superior competitors by growing quickly enough to maintain their feeding end clear (Osman 1977).

The importance of competition for structuring epifaunal communities of estuaries is poorly known. Competition may be important because epifaunal animals in estuaries tend to recruit at high densities, grow rapidly, and often completely cover hard substrates (personal observation), suggesting that space may be limiting (see chapter 3). Studies in other types of systems have shown that competition is likely to be strongest when species are growing rapidly (Huston 1979) and recruiting at high densities (Menge and Sutherland 1987). Recruitment, growth and percent cover in Chesapeake Bay epifaunal communities peaks in May to September (Abbe 1987), suggesting that competition may be strongest in summer.

Since hypoxia is a common stress in summer for epifaunal communities in the York River (Kuo and Neilson 1987, see chapter 1), it may alter the importance of competition in determining community composition and abundance of species. Hypoxia decreases predation (Nestlerode and Diaz 1998, and see chapter 2), which could increase the importance of competition (Menge and Sutherland 1987). However, hypoxia is also likely to decrease growth of epifaunal animals and increase disturbance (Forbes and Lopez 1990, Diaz and Rosenberg 1995), slowing the rate of competitive displacement (Huston 1979, Menge and Sutherland 1987).

The objectives of this study were to examine 1) whether competition is an important process that structures epifaunal communities in the York River, 2) which species are strongest competitors for space, and 3) whether oxygen stress affects the importance of competition in York River epifaunal communities.

Methods

Correlative evidence

Species that compete are likely to be negatively correlated in space. I examined correlations among dominant species (species that covered greater than 5% of space) in the percent cover on settling panels in York River (see chapter 1 for description of panels, deployment dates, and other experimental details) in the summers of 1996 and 1997. For each month of the study (May - September each year), I calculated the Pearson product moment correlation (Sokal and Rohlf 1981) for all possible pairs of dominant species. Correlations were calculated for all panels (upstream and downstream) combined. To explore the possible effects of hypoxia on competition, I also calculated correlations for upstream and downstream panels separately, because the downstream area often experienced lower oxygen concentrations than the upstream area during hypoxic episodes (see chapters 1 and 3).

Competitor removal experiments

If two epifaunal species compete, they can each be expected to occupy a greater percentage of space in the absence of their competitor. I tested for competition among York River species by removing a selected species from experimental panels and observing the change in percent cover of other species. PVC panels (10 X 10 cm) were suspended from the VIMS oyster pier at a depth of 2-3 m on 4 June, 1998. On 24 August, 1998, I retrieved these panels and determined the percent cover of sessile species using a point sampling technique (Sutherland and Karlson 1977), in which live animals under 100 random points were identified to the lowest possible taxon using a dissecting microscope. When more than one species fell under a point, I counted all species; thus, percent cover could exceed 100%. The following species dominated the panels: bryozoan *Membranipora tenuis* , polychaetes *Polydora cornuta* and *Sabella microphthalma*, tunicate *Molgula manhattensis*,

hydroid *Obelia bicuspidata* and anemone *Diadumene leucolena*. Together, these species covered 119.96 ± 18.19% of space on panels (mean ± standard deviation), while empty space covered only 6.82 ± 5.06% of space, and other species covered 6.36 ± 4.28% .

In the laboratory, for each of the 6 dominant species named above, I used 10 randomly assigned panels to test the effect of removing that species. Each panel was divided into halves; one half (control) remained intact while the species of interest was removed from the other half (removal) using a spatula or forceps (Fig. 1). For two species, *Polydora cornuta* and *Obelia bicuspidata*, complete removal was difficult without damaging other species. *P. cornuta* tubes were closely intertwined with tubes and stolons of other species, and removing *P. cornuta* tubes may have damaged other species in *P. cornuta* removals. Therefore, the results of the *P. cornuta* removals should be interpreted cautiously. Similarly, stolons of the hydroid *Obelia bicuspidata* often grew underneath other species; since it was not possible to remove stolons without also removing other animals, instead I cut stolons as close to the base as possible using scissors. In addition to removing target species from half of each panel, I removed all species from a 1 cm wide barrier between the control and removal sections (Fig. 1). I determined the percent cover of each species on control and removal sections of panels using a point sampling technique (Sutherland and Karlson 1977). After less than 1 day in the laboratory, I re-suspended panels from the VIMS pier for 2 weeks, and subsequently retrieved them and again determined the percent cover of each species on control and removal sections.

For each panel, I calculated the change in percent cover of the six dominant species on control and removal areas during the experiment by subtracting percent cover at the beginning from the percent cover at the end of the experiment. For each treatment, I tested the effect of removing a potential competitor by comparing the change in percent cover of the five remaining dominant species in control and removal areas using MANOVA (I did not include the species which was removed in these analyses, because I was testing for interspecific competition). To check the assumptions of MANOVA (Scheiner 1993), a

Cochran's test for homogeneity of variance (Underwood 1997) and a Shapiro-Wilkes test for normality (Zar 1996) were performed for each species. If a species did not meet the assumptions of normality and homogeneity of variance, I transformed the data by arcsin (squareroot(x)) and tested again for normality and homogeneity of variance (Zar 1996). MANOVAs were only performed after all species met each assumption.

Results

Correlative evidence

There were few significant correlations between species at the nominal (pairwise) α of 0.05 (18 of 133) in 1996 and 1997 when all panels (upstream and downstream) were combined (Table 1, Appendix 1). Significant correlations were about as likely to be positive (10 of 16) as negative (8 of 16) (Table 1, Appendix 1). In 1996, 1 positive and 2 negative correlations out of 46 were nominally significant, and these occurred in July (Table 1, Appendix 1). In 1997, 9 positive and 6 negative correlations of 87 were significant, and again more than half of these occurred in July (Table 1, Appendix 1).

During both years, there were similar numbers of nominally significant correlations in the upstream (1 in 1996, 8 in 1997) and downstream (2 in 1996, 5 in 1997) areas (Table 1, Appendix 1), even though these areas differed in oxygen concentration during hypoxic episodes (see chapter 1). When I considered only panels from the upstream area, 1 of 46 correlations was significant in 1996, and this correlation was positive (Table 1, Appendix 1). In 1997, 8 of 87 correlations in the upstream area were significant, and only 3 of these were negative (Table 1, Appendix 1). In the downstream area, where oxygen concentrations tended to be lower during hypoxic episodes (see chapters 1 and 3), again there were few significant correlations (Table 1, Appendix 1). In 1996, 2 (1 positive and 1 negative) correlations out of 46 were significant downstream (Table 1, Appendix 1). In 1997, 5 of 87

correlations were significant downstream, and all of these were positive correlations (Table 1, Appendix 1).

Since I performed a large number of tests, it is likely that some correlations were significant merely by chance (Sokal and Rohlf 1981). Of 133 correlations for upstream and downstream combined, only 6% were significantly negative, similar to the expected percentage of Type I error (Sokal and Rohlf 1981). Less than 8% of correlations were significantly positive. Therefore, correlations provided no compelling evidence for negative or positive associations among York River epifaunal species.

Competitor removal experiments

There were no significant differences between controls and removals for five of the six species tested as possible competitors (Table 2, Fig. 2). In the *Polydora cornuta* treatment, there was a significant difference between controls and removals, but it was mainly due to a decrease in cover of *Membranipora tenuis* in removals, rather than increases in cover of possible competitors with *P. cornuta* (Table 2, Fig. 2). For *Diadumene leucolena*, *Polydora cornuta*, *Sabella microphthalma* and *Molgula manhattensis* there was little change in percent cover in any treatments, with less than 10% change in all cases except one (*P. cornuta* increased 25% when it was removed). The hydroid *Obelia bicuspidata* increased cover by 15-50% in all treatments, with few differences between controls and removals except in the *O. bicuspidata* removal, where it increased by approximately 30% more than in the control. The bryozoan *Membranipora tenuis* showed either little change in cover or a decrease in cover in all treatments except when it was removed, in which case its percent cover increased by 25%.

Discussion

There was little evidence of competition between dominant sessile species in the York River epifaunal community. There were few significant negative correlations between species in the field during any month of our study, for all stations combined or for upstream and downstream areas separately. For each treatment in the removal experiment, the main effect of removing a possible competitor was that the species removed recovered quickly, while other species were largely unaffected. These results contrast greatly with many studies where investigators found significant evidence for competition in epifaunal communities (Connell 1961, Dayton 1971, Jackson 1977, Osman 1977, Hart and Grosberg 1999, but see Turner and Todd 1993 and Brown and Swearingen 1998).

There are many possible reasons why competition may be less important in the York River than in other areas. First, occupation of space by one species does not necessarily inhibit occupation by another; instead I have often observed different species using the same primary space, suggesting that they may not compete for space (Fig. 3). For example, bryozoans (including *Membranipora tenuis*) often cover worm tubes, barnacle tests, tunicates, and hydroid stolons; in each case the other species can keep the feeding end clear of bryozoan (Fig. 3 a, c and e). Similarly, *Polydora cornuta* frequently builds tubes on bryozoans, other worm tubes, tunicates, and around the stolons of hydroids, yet the other species survive (Fig. 3 b, c and d). Worm tubes, hydroids, and anemones often foul the tunics of *Molgula manhattensis*, yet heavily fouled tunicates remain healthy, growing large (>4 cm long) and carrying numerous eggs and sperm (personal observation), possibly because they can extend their siphons beyond competitors (Fig. 3 d). Similarly, Schiaparelli and Cattaneo-Vietti (1999) observed that tube-dwelling vermetid gastropods do not compete for space, but rather continually re-orient tubes to keep the feeding ends clear of obstacles and competitors. One exception to the observation that York River epifaunal species can often share space may occur when young recruits meet adults; I have observed

small barnacles (< 3 mm basal diameter), tunicates (< 5 mm) and *P. cornuta* tubes (< 3 mm long) completely overgrown by bryozoans. Possibly, small recruits can't grow quickly enough to avoid being smothered by competitors. Others have also found that competitive ability depends on developmental stage and body size (Sutherland 1978).

A second reason for the apparent unimportance of competition in this study is that, in some epifaunal communities, seasonal variation in recruitment rather than competition determined community structure (Turner and Todd 1993, Brown and Swearingen 1998). In these communities, space was not limiting (because there was abundant bare space) and assemblages were dominated by the species that were recruiting (Turner and Todd 1993, Brown and Swearingen 1998). Dominance in York River epifaunal communities may also be determined by recruitment. For example, in the removal experiment, *Obelia bicuspidata* was the only species that consistently increased in percent cover, and it recruits most heavily in late August when the experiment was conducted (see chapter 3). If space is not limiting because species can share space (Fig. 3), then seasonal recruitment could become much more important in structuring communities than competition.

Third, estuarine epifauna might not have evolved adaptations that make good competitors. For example, some authors have suggested that estuarine epifauna, which evolved to use transient substrates such as oyster shells, might be optimized for colonizing space but not for competing (Wells 1961, Sutherland and Karlson 1977). Species adapted to tolerate stress generally are not good competitors (Grime 1973); estuaries are highly stressful environments and epifauna that are adapted to withstand highly variable salinity, temperature and other stresses may not be adapted for capturing and holding space. Also, the best competitors in epifaunal communities are usually colonial species (Jackson 1977, Buss and Jackson 1979), but only 36% of recorded sessile species in the York River epifaunal community are colonial (see chapter 1).

Fourth, competition in the removal experiment might have been reduced if the species we studied were not actively recruiting or growing during the study period.

Epifaunal communities in the Chesapeake Bay reach a peak in biomass in August and then biomass begins to decline in September (Abbe 1987). The competitor removal experiment may have occurred after the community was starting to decline. Two of the six dominant species, *Polydora cornuta* and *Membranipora tenuis* , have recruitment peaks in June and July in the York River, but both continue to recruit at lower densities during August (chapter 3). Three of the six dominant species (*Diadumene leucolena*, *Obelia bicuspidata* and *Molgula manhattensis*) have maximal recruitment in mid to late August, and may have recruited in high numbers during this experiment. However, recruitment often occurs in short, discrete pulses, and it is possible that none of these pulses occurred during this experiment. Of the six dominant species, three (*Membranipora tenuis* , *Diadumene leucolena* and *Obelia bicuspidata*) reach maximal percent cover in August, suggesting that they may have actively grown during the competitor removal experiment, while *Polydora cornuta* declines in late summer and *Molgula manhattensis* has more variable peaks in percent cover (chapter 1). For all treatments, the species that was removed reclaimed space, suggesting that all species were either growing, recruiting, or both, and so could have been competing for space.

It is also possible that I didn't find competition in these experiments because I didn't use the right kinds of communities or because manipulations were inadequate. Correlations did not directly test for competitive interactions, and data for correlations came from panels that were only 1 month old. Possibly, competition is more important on older panels. However, the removal experiment used panels that were 2 months old and still failed to find direct evidence of competition. Some manipulations weren't complete, for example, many hydroid stolons remained on hydroid removal plates, and efforts to remove *Polydora cornuta* may have either missed some tubes or inadvertently damaged other species. The fact that species were so closely intertwined, however, that they were difficult to extricate from other species, suggests these animals live closely together and share space.

Because correlations showed provided little evidence for competition in either upstream or downstream communities in the field, it is difficult to speculate how hypoxia might affect the importance of competition in York River epifaunal communities. Menge and Sutherland (1987) suggest that stress can have one of two effects on the importance of competition. Stress can increase the importance of competition, if decreased predation allows good competitors to capture more space, but stress also could decrease the importance of competition, because increased disturbance might create free space (Menge and Sutherland 1987). Since many predators are relatively intolerant of low oxygen, and hypoxia decreases predation rates by many epifaunal predators (Nestlerode and Diaz 1998, and see chapter 3), reduced predation during hypoxia could lower mortality of some competitors and increase the importance of competition. However, at least some species of predators that stop feeding during hypoxia show accelerated feeding following hypoxia (see chapter 2), and so effects of reduced predation are likely to be short-lived. In contrast, hypoxia could increase disturbance, thereby freeing space and decreasing the importance of competition, but many epifaunal species in the York River are highly tolerant of low oxygen and would not experience high mortality during typical hypoxic episodes (see chapter 2). In addition, many animals reduce growth during hypoxia, (Forbes and Lopez 1990, Diaz and Rosenberg 1995, and see chapter 3), reducing the ability of potential competitors to capture space. It seems most likely that decreased growth and possible disturbance could decrease the importance of competition during hypoxic episodes, while reduced predation pressures may increase the importance of competition between hypoxic episodes, but this increase may be short-lived.

Table 1. Summary of results of Pearson product moment correlations between pairs of dominant species in 1996 and 1997, considering all stations combined and upstream and downstream separately.

	number of correlations calculated	number positive with α <0.05	number negative with α <0.05
All stations combined:			
1966	46	1	2
1997	87	9	6
Upstream only:			
1996	46	1	0
1997	87	5	3
Downstream only:			
1996	46	1	1
1997	87	5	0

Table 2. MANOVAs comparing the change in percent cover of the six dominant species in control and removal areas.

Species Removed	Wilks Lamda	df (numerator, denominator)	F	p
Diadumene leucolena	0.843	5, 14	0.445	0.809
Membranipora tenuis	0.801	5, 14	0.594	0.705
Molgula manhattensis	0.916	5, 14	0.257	0.929
Obelia bicuspidata	0.566	5, 14	1.84	0.179
Polydora cornuta	0.471	5, 14	3.144	0.041
Sabella microphthalma	0.823	5, 14	0.603	0.679

Fig. 1. Schematic of panels in competitor removal experiment, showing control and removal areas.

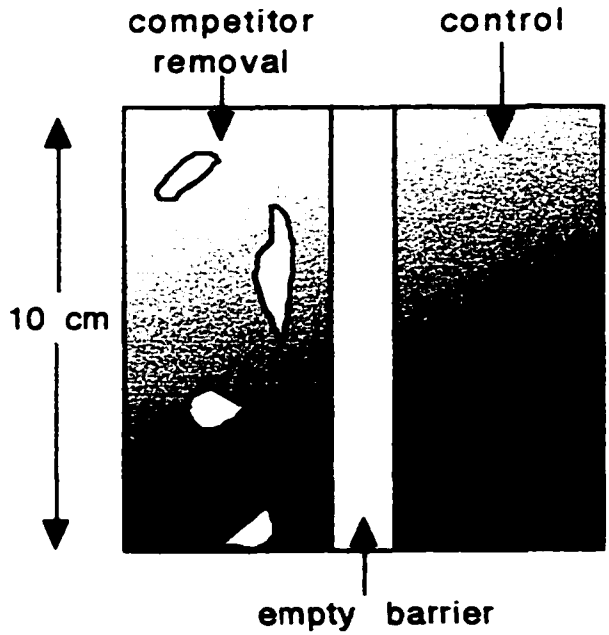


Fig. 2. Results of competitor removal experiment. Each panel shows a different treatment (different species removed) and the change in percent cover of the six dominant species during the experiment (mean ± 1 standard error). P-values are for MANOVAs comparing the effect of a species removal on the five other dominant species.

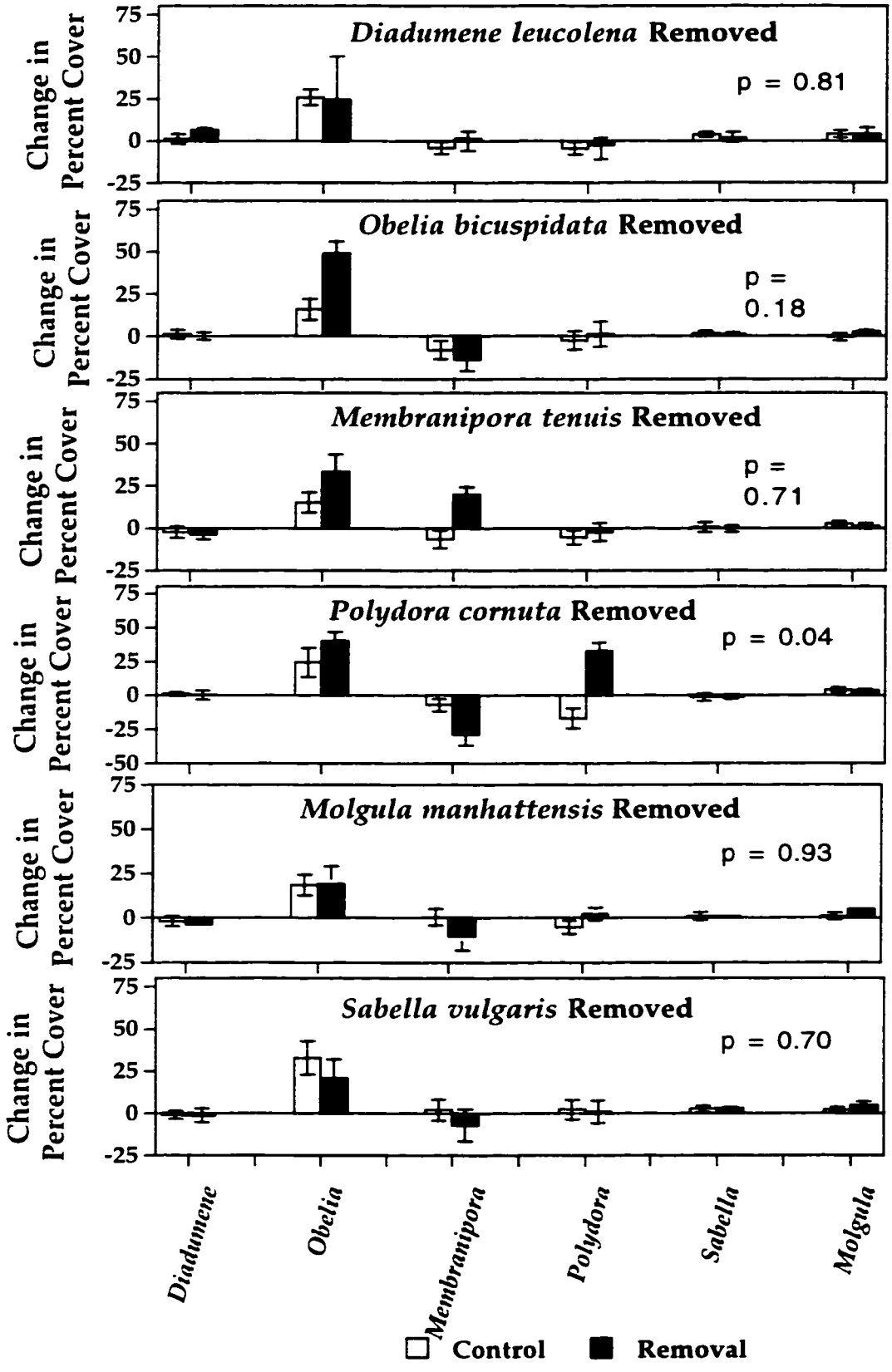
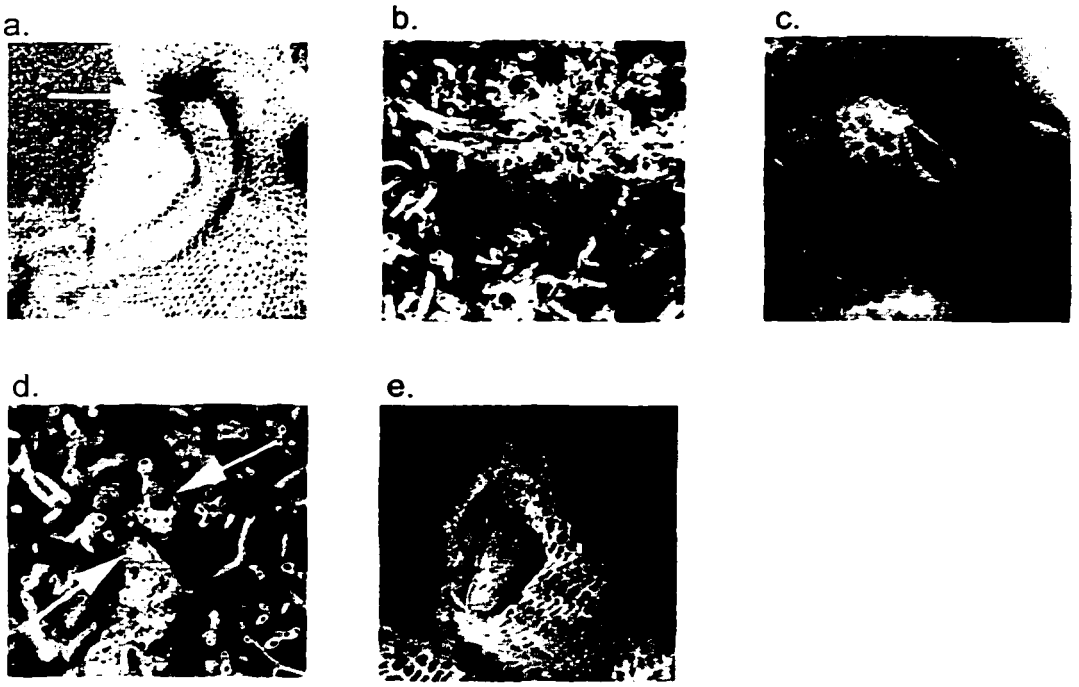


Fig. 3. Examples of epifaunal species occupying space without excluding each other. a. Polychaete *Sabellaria vulgaris* tube completely covered by a bryozoan, with feeding end (arrow) clear. b. Anemone *Diadumene leucolena* surrounded by *Polydora cornuta* tubes and the tunicate *Molgula manhattensis*. c. Barnacle *Balanus improvisus* covered on one half by bryozoans and on the other half by *Polydora cornuta* tubes. d. Siphons of the tunicate *Molgula manhattensis* (arrows), surrounded by *Polydora cornuta* tubes. e. *Balanus improvisus* covered by bryozoan on shell plates, but not on valves.



Appendix 1. Pearson product moment correlations for all pairs of dominant species in 1996 and 1997 for a) all stations combined, b) upstream and downstream separately.

a. June 1996

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*
Balanus improvisus	-0.047 (NS)		
Conopeum tenuissimum	-0.702 (NS)	-0.166 (NS)	
Molgula manhattensis	0.522 (NS)	-0.021 (NS)	-0.245 (NS)

July 1996

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*	*Sabellaria vulgaris*
Balanus improvisus	-0.657 (0.04)				
Conopeum tenuissimum	-0.748 (0.01)	0.316 (NS)			
Molgula manhattensis	0.309 (NS)	-0.106 (NS)	-0.346 (NS)		
Sabellaria vulgaris	-0.602 (NS)	0.523 (NS)	0.729 (0.02)	-0.186 (NS)	
Obelia bicuspidata	0.336 (NS)	-0.329 (NS)	-0.295 (NS)	-0.369 (NS)	-0.459 (NS)

August 1996

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Diadumene leucolena*
Molgula manhattensis	0.572 (NS)				
Obelia bicuspidata	0.421 (NS)	0.324 (NS)			
Sabellaria vulgaris	0.175 (NS)	-0.294 (NS)	-0.470 (NS)		
Diadumene leucolena	-0.349 (NS)	-0.590 (NS)	0.071 (NS)	0.218 (NS)	
Membranipora tenuis	-0.373 (NS)	-0.486 (NS)	0.311 (NS)	-0.203 (NS)	0.399 (NS)

September 1996

	Polydora cornuta	*Molgula manhattensis*	*Membranipora tenuis*	*Diadumene leucolena*
Molgula manhattensis	-0.055 (NS)			
Membranipora tenuis	0.040 (NS)	0.032 (NS)		
Diadumene leucolena	0.131 (NS)	0.220 (NS)	0.153 (NS)	
Ectopleura dumortieri	-0.153 (NS)	0.581 (NS)	0.006 (NS)	-0.169 (NS)

June 1997

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*
Balanus improvisus	.029 (NS)			
Conopeum tenuissimum	-0.166 (NS)	-0.253 (NS)		
Molgula manhattensis	0.113 (NS)	0.536 (0.02)	0.264 (NS)	
Membranipora tenuis	-0.117 (NS)	-0.037 (NS)	0.393 (NS)	0.147 (NS)

July 1997

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Membranipora tenuis*
Balanus improvisus	0.099 (NS)						
Conopeum tenuissimum	-0.492 (NS)	-0.181 (NS)					
Molgula manhattensis	0.478 (NS)	-0.140 (NS)	-0.755 (0.001)				
Obelia bicuspidata	0.625 (0.01)	-0.141 (NS)	-0.566 (0.02)	0.466 (NS)			
Sabellaria vulgaris	-0.436 (NS)	0.174 (NS)	0.620 (0.01)	-0.544(0.03)	-0.358 (NS)		
Membranipora tenuis	-0.392 (NS)	-0.010 (NS)	0.726 (0.002)	-0.603(0.01)	-0.353 (NS)	0.845 (0.0001)	
Diadumene leucolena	0.534 (0.03)	-0.152 (NS)	0.079 (NS)	0.099 (NS)	0.224 (NS)	-0.095 (NS)	-0.081 (NS)

August 1997

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Membranipora tenuis*	*Diadumene leucolena*	*Ectopleura dumortieri*
Molgula manhattensis	0.176 (NS)						
Obelia bicuspidata	-0.018 (NS)	-0.155 (NS)					
Sabellaria vulgaris	-0.413 (NS)	-0.369 (NS)	-0.391 (NS)				
Membranipora tenuis	-0.422 (NS)	-0.534 (0.03)	-0.225 (NS)	0.722 (0.001)			
Diadumene leucolena	0.168 (NS)	-0.471 (NS)	0.480 (NS)	-0.036 (NS)	0.096 (NS)		
Ectopleura dumortieri	0.255 (NS)	0.113 (NS)	0.025 (NS)	-0.052 (NS)	-0.147 (NS)	-0.331 (NS)	
Hydroides dianthus	0.519 (0.04)	-0.222 (NS)	-0.122 (NS)	-0.250 (NS)	-0.059 (NS)	0.204 (NS)	0.153 (NS)

September 1997

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Membranipora tenuis*	*Diadumene leucolena*	*Ectopleura dumortieri*
Molgula manhattensis	-0.283 (NS)					
Obelia bicuspidata	-0.295 (NS)	0.097 (NS)				
Membranipora tenuis	-0.403 (NS)	-0.053 (NS)	-0.376 (NS)			
Diadumene leucolena	-0.351 (NS)	0.224 (NS)	0.421 (NS)	0.044 (NS)		
Ectopleura dumortieri	0.194 (NS)	-0.525 (0.04)	0.169 (NS)	-0.247 (NS)	-0.125 (NS)	
Hydroides dianthus	0.553 (0.03)	0.135 (NS)	-0.132 (NS)	-0.023 (NS)	-0.221 (NS)	-0.176 (NS)

b. Upstream June 1996

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*
Conopeum tenuissimum	-0.640 (NS)		
Balanus improvisus	0.244 (NS)	-0.376 (NS)	
Molgula manhattensis	0.037 (NS)	0.253 (NS)	0.022 (NS)

Downstream June 1996

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*
Conopeum tenuissimum	-0.389 (NS)		
Balanus improvisus	-0.153 (NS)	0.393 (NS)	
Molgula manhattensis	-0.096 (NS)	-0.060 (NS)	0.338 (NS)

Upstream July 1996

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*	*Sabellaria vulgaris*
Balanus improvisus	-0.308 (NS)				
Conopeum tenuissimum	-0.456 (NS)	-0.391 (NS)			
Molgula manhattensis	0.603 (NS)	-0.337 (NS)	-0.728 (NS)		
Sabellaria vulgaris	0.571 (NS)	-0.136 (NS)	0.283 (NS)	-0.303 (NS)	
Obelia bicuspidata	-0.516 (NS)	-0.442 (NS)	0.989 (NS)	-0.663 (NS)	0.15 (NS)

Downstream July 1996

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*	*Sabellaria vulgaris*
Balanus improvisus	0.200 (NS)				
Conopeum tenuissimum	-0.542 (NS)	0.036 (NS)			
Molgula manhattensis	0.483 (NS)	0.203 (NS)	-0.506 (NS)		
Sabellaria vulgaris	-0.673 (NS)	-0.316 (NS)	0.904 (NS)	-0.422 (NS)	
Obelia bicuspidata	-0.063 (NS)	0.437 (NS)	-0.046 (NS)	-0.454 (NS)	-0.347 (NS)

Upstream August 1996

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Diadumene leucolena*
Molgula manhattensis	0.034 (NS)				
Obelia bicuspidata	-0.407 (NS)	-0.405 (NS)			
Sabellaria vulgaris	0.611 (NS)	0.035 (NS)	-0.643 (NS)		
Diadumene leucolena	-0.523 (NS)	-0.731 (NS)	0.316 (NS)	0.034 (NS)	
Membranipora tenuis	-0.547 (NS)	-0.231 (NS)	0.957 (NS)	-0.824 (NS)	0.195 (NS)

Downstream August 1996

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Diadumene leucolena*
Molgula manhattensis	0.975 (NS)				
Obelia bicuspidata	0.819 (NS)	0.858 (NS)			
Sabellaria vulgaris	0.922 (NS)	0.865 (NS)	0.534 (NS)		
Diadumene leucolena	-0.108 (NS)	0.101 (NS)	-0.032 (NS)	-0.106 (NS)	
Membranipora tenuis	-0.052 (NS)	0.155 (NS)	0.004 (NS)	-0.048 (NS)	0.998 (0.002)

Upstream September 1996

	Polydora cornuta	*Molgula manhattensis*	*Membranipora tenuis*	*Diadumene leucolena*
Molgula manhattensis	0.402 (NS)			
Membranipora tenuis	0.739 (NS)	-0.223 (NS)		
Diadumene leucolena	0.645 (NS)	0.688 (NS)	-0.009 (NS)	
Ectopleura dumortieri	0.274 (NS)	0.979 (0.02)	-0.279 (NS)	0.527 (NS)

Downstream September 1996

	Polydora cornuta	*Molgula manhattensis*	*Membranipora tenuis*	*Diadumene leucolena*
Molgula manhattensis	-0.240 (NS)			
Membranipora tenuis	-1.00 (0.0001)	0.240 (NS)		
Diadumene leucolena	0.500 (NS)	-0.961 (NS)	-0.500 (NS)	
Ectopleura dumortieri	-0.898 (NS)	0.643 (NS)	0.898 (NS)	-0.830 (NS)

Upstream June 1997

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*
Balanus improvisus	0.410 (NS)			
Conopeum tenuissimum	-0.331 (NS)	-0.029 (NS)		
Molgula manhattensis	0.236 (NS)	0.246 (NS)	0.603 (NS)	
Membranipora tenuis	0.095 (NS)	-0.064 (NS)	0.247 (NS)	0.039 (NS)

Downstream June 1997

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*
Balanus improvisus	-0.313 (NS)			
Conopeum tenuissimum	0.492 (NS)	-0.214 (NS)		
Molgula manhattensis	0.026 (NS)	0.848 (0.01)	-0.316 (NS)	
Membranipora tenuis	-0.059 (NS)	0.752 (0.03)	-0.129 (NS)	0.670 (NS)

Upstream July 1997

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Membranipora tenuis*
Balanus improvisus	-0.485 (NS)						
Conopeum tenuissimum	-0.168 (NS)	0.637 (NS)					
Molgula manhattensis	-0.040 (NS)	-0.451 (NS)	-0.908 (0.002)				
Obelia bicuspidata	0.281 (NS)	0.281 (NS)	-0.204 (NS)	0.147 (NS)			
Sabellaria vulgaris	-0.323 (NS)	0.934 (0.001)	0.573 (NS)	-0.451 (NS)	-0.237 (NS)		
Membranipora tenuis	-0.311 (NS)	0.733 (0.04)	0.667 (NS)	-0.653 (NS)	-0.165 (NS)	0.845 (0.01)	
Diadumene leucolena	-0.644 (NS)	0.655 (NS)	0.751 (0.03)	-0.627 (NS)	-0.311 (NS)	0.498 (NS)	0.624 (NS)

Downstream July 1997

	Polydora cornuta	*Balanus improvisus*	*Conopeum tenuissimum*	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Membranipora tenuis*
Balanus improvisus	-0.246 (NS)						
Conopeum tenuissimum	0.490 (NS)	-0.444 (NS)					
Molgula manhattensis	0.498 (NS)	-0.395 (NS)	0.118 (NS)				
Obelia bicuspidata	0.005 (NS)	-0.662 (NS)	-0.293 (NS)	0.441 (NS)			
Sabellaria vulgaris	-0.472 (NS)	0.123 (NS)	0.000 (NS)	-0.671 (NS)	-0.373 (NS)		
Membranipora tenuis	0.396 (NS)	-0.328 (NS)	0.316 (NS)	0.280 (NS)	0.100 (NS)	0.255 (NS)	
Diadumene leucolena	0.511 (NS)	-0.420 (NS)	0.859 (0.006)	0.096 (NS)	-0.142 (NS)	-0.277 (NS)	-0.099 (NS)

Upstream August 1997

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Membranipora tenuis*	*Diadumene leucolena*	*Ectopleura dumortieri*
Molgula manhattensis	0.339 (NS)						
Obelia bicuspidata	-0.087 (NS)	0.140 (NS)					
Sabellaria vulgaris	-0.272 (NS)	-0.735 (0.04)	-0.535 (NS)				
Membranipora tenuis	-0.349 (NS)	-0.781 (0.02)	-0.534 (NS)	0.698 (NS)			
Diadumene leucolena	-0.335 (NS)	-0.499 (NS)	0.627 (NS)	0.103 (NS)	0.006 (NS)		
Ectopleura dumortieri	0.863 (0.006)	-0.047 (NS)	0.087 (NS)	-0.018 (NS)	-0.235 (NS)	0.084 (NS)	
Hydroides dianthus	0.316 (NS)	0.306 (NS)	-0.314 (NS)	-0.104 (NS)	-0.412 (NS)	-0.443 (NS)	0.210 (NS)

Downstream August 1997

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Sabellaria vulgaris*	*Membranipora tenuis*	*Diadumene leucolena*	*Ectopleura dumortieri*
Molgula manhattensis	0.508 (NS)						
Obelia bicuspidata	-0.472 (NS)	-0.278 (NS)					
Sabellaria vulgaris	-0.097 (NS)	0.091 (NS)	-0.075 (NS)				
Membranipora tenuis	-0.449 (NS)	-0.267 (NS)	0.020 (NS)	0.868 (0.005)			
Diadumene leucolena	0.044 (NS)	-0.487 (NS)	0.380 (NS)	0.273 (NS)	0.337 (NS)		
Ectopleura dumortieri	0.129 (NS)	0.337 (NS)	-0.070 (NS)	0.099 (NS)	-0.032 (NS)	-0.596 (NS)	
Hydroides dianthus	0.227 (NS)	-0.396 (NS)	-0.564 (NS)	0.314 (NS)	0.271 (NS)	0.107 (NS)	0.092 (NS)

Upstream September 1997

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Membranipora tenuis*	*Diadumene leucolena*	*Ectopleura dumortieri*
Molgula manhattensis	-0.183 (NS)					
Obelia bicuspidata	-0.105 (NS)	-0.146 (NS)				
Membranipora tenuis	-0.402 (NS)	-0.315 (NS)	-0.529 (NS)			
Diadumene leucolena	-0.209 (NS)	-0.040 (NS)	0.408 (NS)	-0.144 (NS)		
Ectopleura dumortieri	0.061 (NS)	-0.602 (NS)	0.596 (NS)	-0.362 (NS)	-0.076 (NS)	
Hydroides dianthus	-0.438 (NS)	-0.336 (NS)	-0.368 (NS)	0.792 (NS)	-0.219 (NS)	-0.127 (NS)

Downstream September 1997

	Polydora cornuta	*Molgula manhattensis*	*Obelia bicuspidata*	*Membranipora tenuis*	*Diadumene leucolena*	*Ectopleura dumortieri*
Molgula manhattensis	0.173 (NS)					
Obelia bicuspidata	-0.363 (NS)	0.435 (NS)				
Membranipora tenuis	-0.297 (NS)	0.369 (NS)	-0.224 (NS)			
Diadumene leucolena	0.027 (NS)	0.218 (NS)	-0.068 (NS)	0.191 (NS)		
Ectopleura dumortieri	0.034 (NS)	-0.403 (NS)	-0.177 (NS)	0.069 (NS)	0.133 (NS)	
Hydroides dianthus	0.592 (NS)	0.769 (0.03)	-0.014 (NS)	0.176 (NS)	-0.098 (NS)	-0.383 (NS)

GENERAL CONCLUSION

For this dissertation, I tested predictions of the consumer stress model (Menge and Sutherland 1987) in an estuarine epifaunal community that experiences stress from hypoxia. Following are specific predictions of the model and evaluations of whether results support or refute the predictions.

> Prediction 1. Hypoxia will increase mortality and decrease the ability of sessile animals to capture and retain space, leading to lower abundances and lower species diversity in hypoxia than in high oxygen conditions. Species with low tolerance of hypoxia in the laboratory will experience the greatest reduction in abundance in hypoxic field conditions relative to higher oxygen conditions.

As predicted, for at least some species, hypoxia can increase mortality and decrease the ability to capture and retain space. About half of the species studied had LT_{50}s in the lab shorter than the maximum duration of typical hypoxic episodes in the York River, at oxygen concentrations that commonly occur in deep areas of the estuary. This suggests that some species are likely to experience mortality from hypoxia in the field. Hypoxia also decreased the growth of at least one species (*Obelia bicuspidata*) in the lab, suggesting that low oxygen could also impede the ability of some species to capture and retain space. However, most epifaunal species in the York River had high tolerance of hypoxia, and are expected to experience little or no mortality during typical hypoxic episodes in the York River. Hypoxia stress in the York River can be expected to increase disturbance rates, but substantial mortality is unlikely for most species.

In contrast to model predictions, hypoxia had little effect on abundance and diversity in the York River. Hypoxic episodes with dissolved oxygen concentrations ranging from 0.2 mg O_2 / L to 2 mg O_2 / L and lasting 5-7 days occurred regularly throughout each summer in 1996 and 1997, yet epifaunal animals formed dense, spatially complex communities. Distributions of epifaunal species were not correlated with hypoxia tolerance, suggesting that hypoxia was not a major factor determining community structure. Species that were relatively intolerant of hypoxia in laboratory studies (i.e. *Polydora cornuta*) had increased abundance in the downstream study area, where oxygen concentrations were lowest during hypoxic episodes. It seems likely that increased abundance of this species downstream is a result of increased recruitment, rather than to effects of hypoxia on adults. Species with high tolerance of low oxygen in the laboratory (i.e. *Sabellaria vulgaris*, *Membranipora tenuis* , *Conopeum tenuissimum*) were most abundant in the upstream study area, where oxygen was higher during hypoxic episodes. In addition, I found little effect of hypoxia on diversity. Species richness at 15 m, where hypoxia occurred, was similar to richness in shallow, high-oxygen parts of the York River, suggesting that periodic hypoxia, characteristic of the York River, does not exclude most epifaunal species.

The lack of obvious effects of low oxygen stress on epifaunal community structure in the York River may be due to specific characteristics of the York River relative to other hypoxic areas, or to inherent characteristics of epifaunal species in estuaries. The York River is fairly unique among coastal areas in that neap / spring cycles of stratification and destratification limit the duration of hypoxic episodes (Diaz and Rosenberg 1995), limiting the length of exposure to hypoxia by animals. Oxygen concentrations in the York River also vary with flood and ebb tides (Kuo and Neilson 1987), so that each day short intervals of increased oxygen concentrations interrupt the lowest oxygen conditions. In other hypoxic areas, oxygen can remain uniformly low for days or weeks (Diaz and Rosenberg 1995). An additional characteristic of the York River and other estuaries is that currents maintain water movement even during hypoxia, which may increase the flux of oxygen to

animals relative to stagnant conditions, increasing survival. Also, high food availability in estuaries (Kemp et al. 1997) may balance the costs of environmental stress. Characteristics of estuarine epifaunal species that may allow them to survive in hypoxic areas of the York River include generally high tolerance of stress and life history characteristics that allow most species to colonize disturbed areas rapidly, grow quickly, and recover between hypoxic episodes.

> Prediction 2. Predators are highly susceptible to hypoxic stress and have decreased abundances in low oxygen conditions. As a result, predation is less important in low oxygen conditions than in high oxygen conditions.

As predicted, the predators I studied had low tolerance of hypoxia stress relative to many sessile prey species. LT_{50}s calculated from laboratory experiments were low for predators from several phyla even though some of these groups, such as mollusks and turbellarians, are often considered generally tolerant of low oxygen (Mangum and van Winkle 1973, Diaz and Rosenberg 1995). Thus, in this estuarine community, physiological stresses such as hypoxia may have their greatest effects on higher trophic level species, as physical stresses do in rocky intertidal communities.

In spite of generally low tolerance, predators remained abundant in areas of the York River that experience hypoxia, suggesting that hypoxia in this system may not be severe enough or last long enough to kill these species. Predators could also have migrated to shallower areas to avoid hypoxia, and returned when oxygen rose. Although the predators I studied had relatively low mobility, ropes connected stations in the field to surface waters, so predators would not have had to travel far to avoid low oxygen. Laboratory experiments suggested that during hypoxia mobile species climb available objects to reach higher into benthic boundary layers, a behavior that would have facilitated climbing ropes to shallower depths.

Although predators persisted in areas where hypoxia occurred, predation was likely less important to community structure during hypoxic episodes, because hypoxia can decrease predation rates by surviving predators. Thus, this study supported a major contention of consumer stress models, that predation decreases with increasing stress. However, laboratory experiments suggest that decreases in predation due to hypoxia may be brief. At least one predator (mud crab Neopanopeus sayi) can increase predation following short hypoxic episodes, leading to no net decrease in the number of prey consumed. Although low oxygen stress may temporarily decrease predation, communities that experience alternating periods of brief hypoxia and high oxygen could experience little overall change in predation when hypoxic and high-oxygen periods are considered together.

Prediction 3. Recruitment rates are independent of hypoxia.

In the laboratory, hypoxia consistently decreased recruitment of many taxa, suggesting that, in contrast to the prediction, recruitment rates are not independent of environmental stress. However, larvae of these taxa recruited at high rates during hypoxic episodes in the York River. These conflicting results may have occurred because animals react to hypoxia stress in the context of numerous other stresses and forces. In the York River, larval availability, current stress, and other factors probably had greater effects than hypoxia on recruitment. These results suggest that the effects of regional-scale stresses, such as hypoxia, may be particularly difficult to predict from conceptual models because they can vary with numerous other factors. It is also possible that currents maintain a sufficient net flux of oxygen to larvae in the York River, but stagnant conditions in the laboratory don't adequately reflect field conditions.

Prediction 4. Hypoxia will change the importance of competition. If hypoxia decreases predation on dominant space occupiers, it should increase the importance

of competition. If hypoxia increases disturbance and decreases growth, it should decrease the importance of competition.

I was not able to test the effects of hypoxia on competition directly, but I found that competition appears relatively unimportant to York River epifaunal communities in shallow areas, where oxygen remains high. There are several reasons why competition may be less important in this community than in other epifaunal communities. First, occupation of primary space by one species does not necessarily inhibit occupation by another, rather, many species can share primary space by growing on each other. Second, seasonal variation in recruitment may have greater effects than competition on community structure, because species are short-lived. Third, estuarine epifauna may have evolved to colonize free space rapidly, but not to compete over long periods of time for space.

I did determine that hypoxia can decrease predation on dominant space occupiers, and that hypoxia increases disturbance and decreases growth of epifaunal species. So, hypoxia can affect community processes that influence competition. Whether the importance of competition increases or decreases in hypoxic areas depends on the magnitudes of each of these processes.

Summary

This study supported some predictions of the consumer stress model, but not all. I found that as stress increases, the importance of disturbance for determining community structure increases, while the importance of predation decreases. The consumer stress model considers stress and recruitment as independent factors that impact community structure, but this study suggests that stress and recruitment processes can interact. Unlike model predictions, I found few effects of stress on abundance and diversity, possibly because in this system hypoxic stress is relatively mild, is present for short periods of time,

and because the species in this community can tolerate stress, colonize disturbed areas quickly, and grow quickly enough to complete life-cycles between hypoxic episodes.

This dissertation makes a significant contribution towards understanding the ecology of estuaries for two reasons. First, it is among the first studies to apply the consumer stress model to regional-scale, physiological stresses in estuaries. Second, this dissertation helps extend knowledge about the effects of hypoxia on benthic communities by providing information about hypoxia's effects on epifauna, an important component of marine systems.

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